CHAPTER 1-4
AQUATIC AND WET MARCHANTIOPHYTA, ORDER JUNGERMANNIALES: JUNGERMANNIINEAE

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CHAPTER 1-4
AQUATIC AND WET MARCHANTIOPHYTA, ORDER JUNGERMANNIALES: JUNGERMANNIINEAE

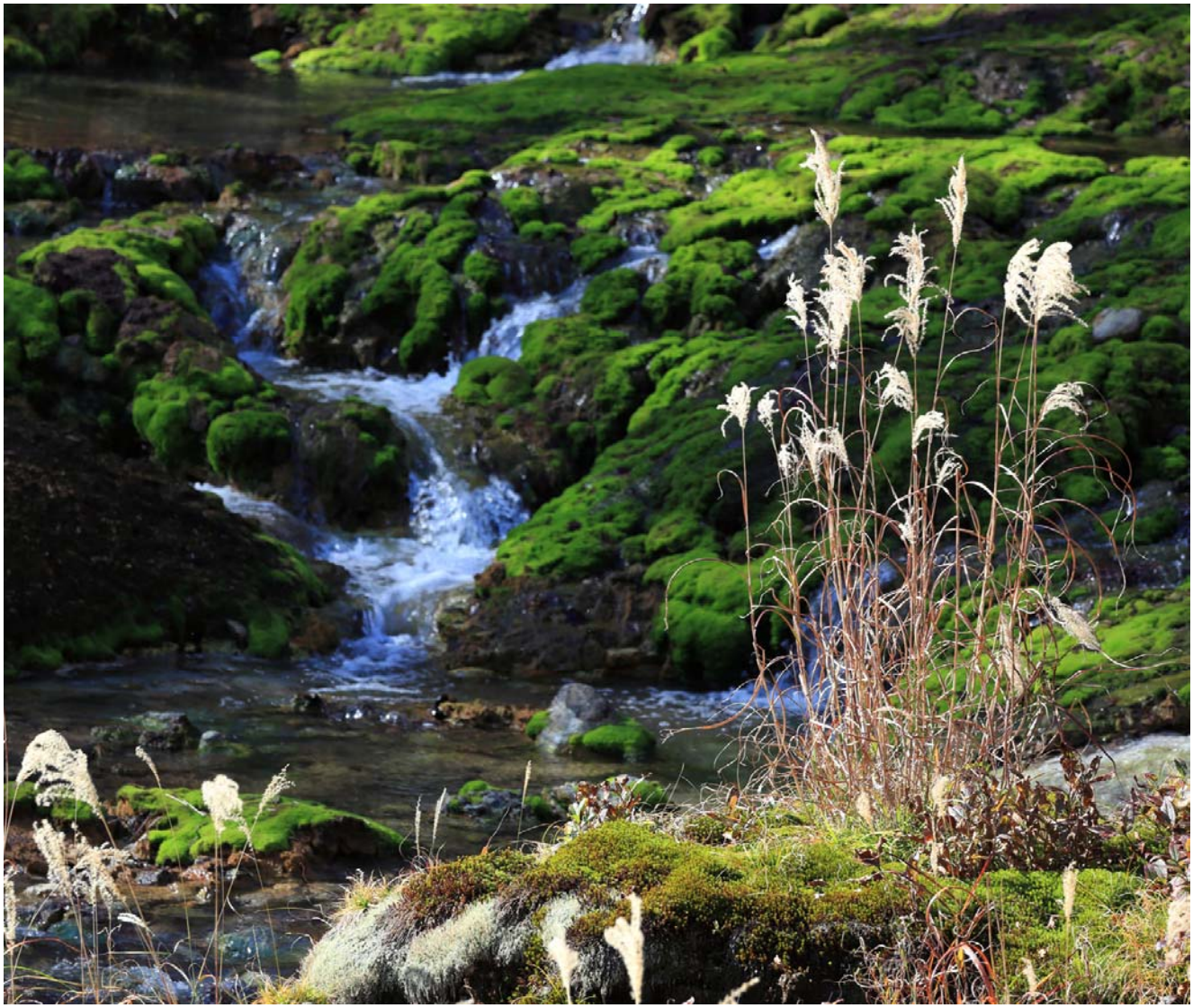

Figure 1. A sulfur stream in Japan where the dominant vegetation is ***Solenostoma vulcanicola***. Photo by Juuyoh Tanaka, through Creative Commons.

Antheliaceae

Anthelia julacea (Figure 2-Figure 3)

Distribution

Anthelia julacea (Figure 2-Figure 3) is somewhat Holarctic, being absent in the northernmost part of the tundra (Schuster 1974). In Europe it extends southward from Iceland to Austria and the Czech Republic in alpine regions. It is present in eastern Siberia, but not in European Russia. It also extends into China, India, and Japan. Its North American distribution is more scattered and rare, with records often proving to be ***Anthelia juratzkana*** (Figure 7-Figure 10). ***Anthelia julacea*** seems to be concentrated on the west coast, from the Aleutian Islands and Alaska southward to Oregon and possibly California. But it is also known from Quebec (Kucyniak 1949).

Figure 2. ***Anthelia julacea***, a holarctic and alpine species common in springs and ***Sphagnum*** hummocks, mixed here with other bryophytes. Photo by Michael Lüth, with permission.

Aquatic And Wet Habitats

West (1910) described this as a species of wet sandy or peaty shores of mountain lakes in Scotland. This liverwort seems to be rather consistently present in the damp tundra (Schuster 1974). In the damp tundra Shimwell (1972) named the ***Anthelion julaceae*** alliance for the sub-alpine spring vegetation dominated by this species. The masses of these liverworts resemble polsters of ***Sphagnum*** hummocks of **ombrogenous** (dependent on rain for its formation) bogs (Figure 3). Jerram (2003) found it in a spring **flush** (area where water from underground flows out onto surface to create area of saturated ground, rather than well-defined channel; piece of boggy ground, especially where water frequently lies on surface; swampy place; pool of water in field) in Cumbria, UK. ***Anthelia julacea*** (Figure 2) occurred with ***Sphagnum auriculatum*** (Figure 4) on flushed slabs of granite. Bajzak and Roberts (2011) found it in tundra-like meadows where ***Sphagnum lindbergii*** (Figure 5) and ***Paludella squarrosa*** (Figure 6) dominated. It covered the ground in some places that were open, forming a dense crust.

Figure 3. ***Anthelia julacea*** forming hummocky mats. Photo by Jean Faubert, with permission.

Figure 4. ***Sphagnum auriculatum***, a species that occurs with ***Anthelia julacea*** on flushed slabs of granite. Photo by Bernd Haynold, through Creative Commons.

Figure 5. ***Sphagnum lindbergii***, a species that occurs with ***Anthelia julacea*** in tundra-like meadows. Photo by J. C. Schou, with permission.

Figure 6. ***Paludella squarrosa***, a species that occurs with ***Anthelia julacea*** in tundra-like meadows. Photo by Hermann Schachner, through Creative Commons.

Adaptations

Anthelia julacea (Figure 2) is a relatively robust plant that occurs in patches or mats (Figure 3). It is typically dark green to deep yellowish green to brown, often is crowded, forming shrub-like mounds.

I have found little information on its photosynthesis and productivity. Dilks and Proctor (1975) found that the photosynthetic response to temperature in ***Anthelia julacea*** (Figure 2) did not differ significantly from that of most lowland species. The species seem to be protected from intracellular freezing to at least -5ºC.

Reproduction

The species is **dioicous** (Jessup 2019), accounting for the fact it is usually lacking sporophytes.

Anthelia juratzkana (Figure 7-Figure 10)

Distribution

Anthelia juratzkana (Figure 7-Figure 10) is mostly Arctic-alpine and bipolar (Schuster 1974). In the Southern Hemisphere it is present in New Zealand, Bolivia, at Tierra del Fuego, Argentina, South Georgia, and Livingston Island, Antarctica. In the Northern Hemisphere, it extends as far northward as the exposed land. It extends southward from there in high alpine summits, extending from Spitsbergen through Scandinavia to England and the central European Alps. In North America it extends southward to Quebec, Canada, and Maine, USA.

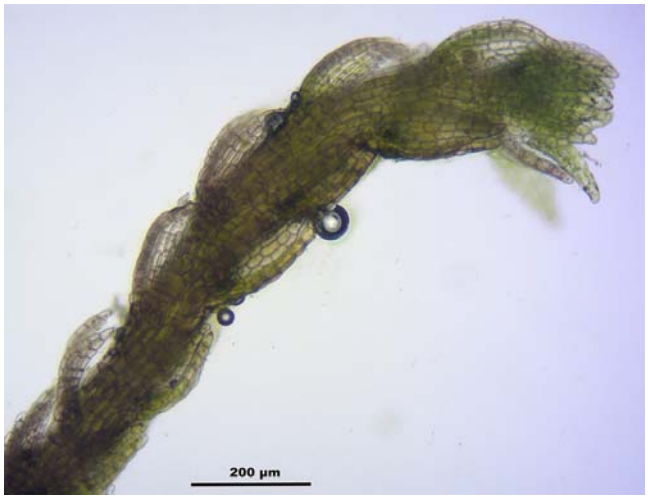

Figure 7. ***Anthelia juratzkana***, an Arctic-alpine and bipolar species that occurs in streams, on the banks of streams and lakes, and on wet cliffs. Photo by Hermann Schachner, through Creative Commons.

Aquatic and Wet Habitats

Anthelia juratzkana (Figure 7-Figure 10) is typical of perennially wet microhabitats (Jessup 2019). Bakalin (2005) found ***Anthelia juratzkana*** (Figure 7-Figure 10) in a sedge-moss mire on Bering Island in northwestern Russia. It also occurred on peaty banks of small lakes with several other leafy liverworts, and on hummocks or hollows in moss-shrub or moss-sedge mires and is also relatively common on the island on peaty banks of lakes, on fine-grained soil in wet crevices, on rocks near small waterfalls, and along streams. It is not common elsewhere in northwestern Asia.

The species is typical of cold, damp sites exposed to full sun for at least part of the growing season (Schuster 1974). It frequently occupies moist, snow-fed slopes (Figure 10) in the Far North. It occurs in alpine streams in the Swiss Alps (Geissler 1976) and on wet cliff and rocks at the lake shore of the Upper Bureya River in the Russian Far East (Konstantinova *et al*. 2002).

Figure 8. ***Anthelia juratzkana*** habitat showing silvery mats. Photo by Michael Lüth, with permission.

Figure 9. ***Anthelia juratzkana*** mats showing closer view with hummocky appearance. Photo by Michael Lüth, with permission.

Figure 10. ***Anthelia juratzkana*** habitat at receding snow bank. Photo by Michael Lüth, with permission.

Role

Anthelia juratzkana (Figure 7) forms thin, silvery gray or decolorate patches on bare ground, sometimes forming dense mounds and appearing bluish gray to gray-green (Schuster 1974). The individual branches are minute.

The bluish coloring is often due to the presence of **Cyanobacteria**. ***Anthelia juratzkana*** (Figure 7-Figure 10) has the blue-green bacterium ***Gloeocapsa montana*** (see Figure 11) associated with it (Riedl 1977). These bacterial colonies give it a gelatinous sheath that causes a waxy, whitish appearance, with a fungus growing in the sheath and another forming a mycorrhiza-like symbiosis with the liverwort.

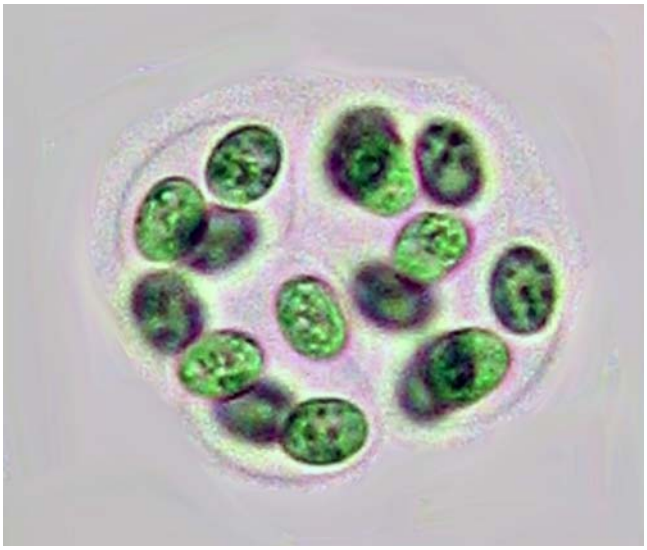

Figure 11. ***Gloeocapsa*** sp.; ***Gloeocapsa montana*** is a **Cyanobacterium** that associates with ***Anthelia juratzkana***. Photo by John, through Creative Commons.

Adaptations

Both species of ***Anthelia*** expresses a variety of phenotypes in response to light, moisture, temperature, and substrate. Both species form lax patches, sods, mounds and **turfs** of elongate stems (2–4 cm) in perennially wet microhabitats.

Lösch *et al*. (1983) found that only the uppermost 4 mm layer of ***Anthelia juratzkana*** (Figure 7-Figure 10) had enough pigment concentration to accomplish photosynthesis. At light saturation, its optimum temperatures were 6-11ºC. In those conditions, maximum CO_2 uptake was 0.7 mg CO_2 g^{-1} dw h^{-1}, compared to 1.5 mg for ***Polytrichastrum sexangulare*** (Figure 12). ***Anthelia juratzkana*** has its low temperature **compensation point** at -4ºC (compensation point is level at which photosynthesis gain is offset by respiration loss). On the other end of the scale, this species cannot sustain photosynthesis at 30ºC. The photosynthetic rate is not damaged by nine months of storage in dark, cold, wet conditions, securing its ability to survive in Arctic and alpine areas.

Reproduction

Anthelia juratzkana is **paroicous** and produces sporophytes frequently (Jessup 2019). It is abundant in the Arctic in midsummer; spore dispersal there occurs as bird migrations begin, increasing opportunities for spores and miniscule stem fragments to be dispersed in the dusted feathers of these birds.

Figure 12. ***Polytrichastrum sexangulare***, a species with a maximum CO_2 uptake of 1.5 mg compared to only 0.7 mg CO_2 g^{-1} dw h^{-1} for ***Anthelia juratzkana***. Photo by Štěpán Koval, with permission.

Balantiopsidaceae

Balantiopsis convexiuscula (Figure 13-Figure 14)

Distribution

Balantiopsis convexiuscula (Figure 13-Figure 14) seems to be restricted to New Zealand and Australia (Simpson 1977; GBIF 2020a).

Figure 13. ***Balantiopsis convexiuscula***, a species of New Zealand and Australia, where it occurs on stream banks, logs, and near waterfalls. Photo by Shirley Kerr, with permission.

Aquatic and Wet Habitats

Balantiopsis convexiuscula (Figure 13-Figure 14) occurs on streambanks in New Zealand (Fineran). Simpson (1971) found it on a bank near a waterfall in Nelson Lakes National Park, New Zealand. Referring to it as **hygrophilic**, Mark *et al*. (1989) noted that it was absent in stands of the Fiord Ecological Region of New Zealand that lacked flowing water. Instead, they are typical in watercourses.

Figure 14. ***Balantiopsis convexiuscula*** forming a vertical mat as one might find on a stream bank. Photo by Shirley Kerr, with permission.

Suren and Duncan (1999) found that ***Balantiopsis convexiuscula*** (Figure 13-Figure 14) is positively correlated with bankfull discharge in their study of 48 streams in South Island, New Zealand. Simpson (1977) found it on logs and on a bank near a waterfall of Coldwater Creek, New Zealand.

Reproduction

Female stems of ***Balantiopsis convexiuscula*** (Figure 13-Figure 14) form an archegonium (Allison & Child 1975). After fertilization, a marsupium forms around the archegonium, from which the capsule emerges. However, capsules are relatively rare. Spores are small.

Calypogeiaceae

Calypogeia (Figure 15-Figure 21, Figure 23-Figure 46)

Geissler (1976) reported ***Calypogeia*** (Figure 15-Figure 21, Figure 23-Figure 46) as ***C. trichomanis*** in alpine streams of the Swiss Alps. Unfortunately, this name has been used for a variety of species and I cannot be sure which one she found. The name is no longer in use.

Stephenson *et al*. (1995) reported ***Calypogeia*** (Figure 15-Figure 21, Figure 23-Figure 46) species from West Virginia, USA, mountain streams. The preferred *p*H was around 5.95.

Calypogeia arguta (Figure 15-Figure 16)

Distribution

Calypogeia arguta (Figure 15-Figure 16) is widely distributed, from the Faeroe Islands and Scandinavia through India, Korea, Japan, and many provinces of China, to South Africa, and New Caledonia (GBIF 2020b). In the Western Hemisphere, it seems to be unknown farther north than Nova Scotia or farther south than Cuba.

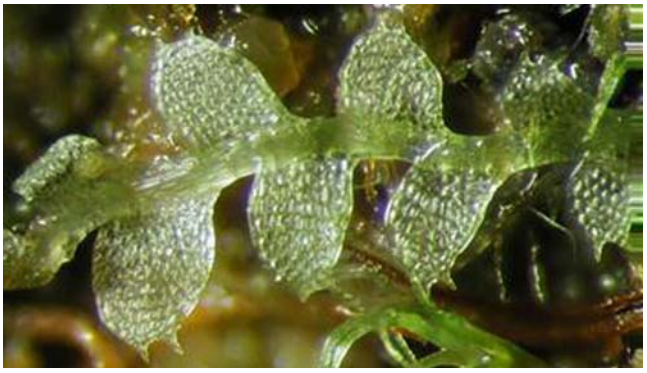

Figure 15. ***Calypogeia arguta***, a widely distributed species in the Northern Hemisphere, of moist soil and wet sites. Photo by Bat Whittler, through Creative Commons.

Aquatic and Wet Habitats

Ferreira *et al*. (2008) reported ***Calypogeia arguta*** (Figure 15) from rivers. ***Calypogeia arguta*** is relatively common on moist soil (Figure 16) in Hong Kong (So & Zhu 1996). It occurs there along with ***Kurzia gonyotricha***, ***Heteroscyphus argutus*** (Figure 17), ***Pallavicinia subciliata*** (Figure 18), and ***Notoscyphus lutescens*** (Figure 19). Those populations vary considerably in size and color. Alam (2011) reports that the species forms smooth mats in the Nilgiri Hills, Tamil Nadu, India. In the Azores, Gabriel and Bates (2005) reported this as a species characteristic of the wettest sites, although it also was most commonly found on rocks.

Figure 16. ***Calypogeia arguta*** habitat at a stream edge on moist soil. Photo by George G., through Creative Commons.

Figure 17. ***Heteroscyphus argutus***, an associate of ***Calypogeia arguta*** in some habitats. Photo by Lin Shanxiong, through Creative Commons.

Figure 18. ***Pallavicinia subciliata***, an associate of ***Calypogeia arguta*** in some habitats. Photo by Lin Shanxiong, through Creative Commons.

Figure 19. ***Notoscyphus lutescens***, an associate of ***Calypogeia arguta*** in some habitats. Photo by David Tng, with permission.

Kitagawa (1978a) considered ***Calypogeia arguta*** (Figure 15-Figure 16) to be a pioneer on the sterile soil of a roadside bank in Mts. Hokkôda, Japan, but also was abundant on soil along sulfur-rich streams.

Adaptations

Its need for water was demonstrated by Clausen (1964). She found that few cells were alive after 12 hours at 20ºC and 93% humidity. At 96% humidity, only about half the cells were alive. But low temperatures are also detrimental; few cells were alive from plants from the Faeroe Islands when subjected to two days on ice at -10ºC.

Reproduction

One possible explanation for the widespread distribution of this species is its ability to survive in diaspore banks. Bisang *et al*. (2003) found that this species germinated from a turf diaspore bank in the Malaysian rainforest.

Fungal Interactions

Calypogeia arguta (Figure 15-Figure 16) is among the liverwort species that apparently inhibit the parasitic ascomycete ***Mniaecia jungermanniae*** (Figure 24-Figure 26) (Pressel & Duckett 2006). Two other liverwort species in the bryophyte association were infected and produced apothecia. Benkert and Otte (2006), on the other hand, observed ***M. jungermanniae*** using ***Calypogeia arguta*** as host. The fungus is most common in the colder periods of the year (March to May) in the Liberec Region of the Czech Republic (Egertová *et al*. 2016).

Calypogeia azurea (Figure 20-Figure 21)

Distribution

Calypogeia azurea (Figure 20-Figure 21) is a widespread, subboreal-montane species (Buczkowska *et al*. 2016), being widely distributed through the northern hemisphere, including North America (rare; in Pacific Northwest), Europe, and eastern Asia (Buczkowska *et al*. 2018).

Figure 20. ***Calypogeia azurea***, a species widely distributed in the Northern Hemisphere. Photo by Hermann Schachner, through Creative Commons.

Figure 21. ***Calypogeia azurea*** showing gemmae. Photo by Hermann Schachner, through Creative Commons.

Aquatic and Wet Habitats

It occurs on loamy soil, humus, peat, wet stones and rocks, to rotten logs (Buczkowska *et al*. 2018). Watson (1919) considered it (as *Calypogeia trichomanis*) to be a

species of stream or river banks that experienced frequent submergence and slow water. Thus, the populations would occasionally become submerged. Geissler and Selldorf (1986) reported it occurring with *Carex goodenoughii* and uncommonly with ***Eleocharis quinqueflora*** (Figure 22) in European mountains.

Figure 22. ***Eleocharis quinqueflora***, a sedge species that sometimes has ***Calypogeia azurea*** at its base. Photo by Max Licher, through Creative Commons.

In the ***Calypogeia azurea*** complex, ***C. sinensis*** prefers wet open cliffs and partly shaded cliff caves in the waterfall spray zone, or mesic tree trunk bases and decaying wood in broad-leaved, evergreen, subtropical to southern subtropical montane forests (Buczkowska *et al*. 2018). It has only two known localities. The first is subtropical montane forest near Xiniu Waterfall in the Chinese province of Guizhou at about 1300 m asl. The second locality is a subtropical montane forest in southern North Vietnam, at about 2000 m asl.

Adaptations and Variations

Calypogeia azurea (Figure 20-Figure 21) is one of the few members of ***Calypogeia*** that has blue oil bodies (Figure 23) (Buczkowska *et al*. 2016), giving it a bluish color and accounting for the epithet *azurea*. The species presents a variety of environmentally induced morphological differences.

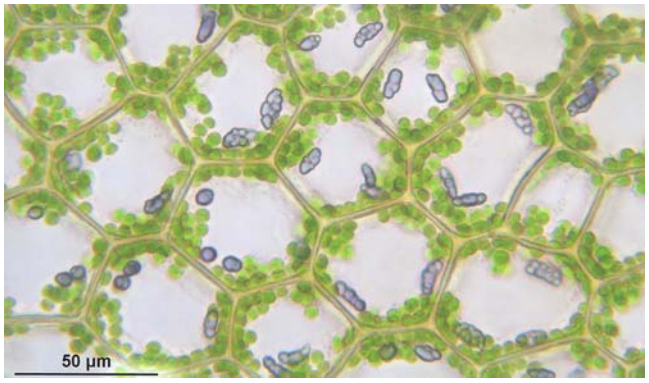

Figure 23. ***Calypogeia azurea*** leaf cells showing bluish oil bodies. Photo by Hermann Schachner, through Creative Commons.

Reproduction

Calypogeia azurea (Figure 20-Figure 21) is **autoicous** (Paton 1999; Damsholt 2002), although Damsholt also questions the possibility it is sometimes **paroicous**.

Fungal Interactions

Calypogeia azurea (Figure 20-Figure 21) is a species where the fungal parasite ***Mniaecia jungermanniae*** (Figure 24-Figure 26) finds suitable habitat and host (Egertová *et al*. 2016). These occurrences include liverworts growing on wet soil.

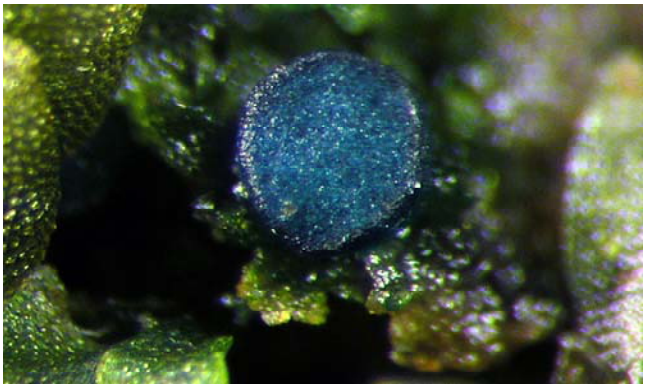

Figure 24. ***Calypogeia azurea*** with fungal parasite ***Mniaecia jungermanniae***. Photo by Walter Obermayer, with permission.

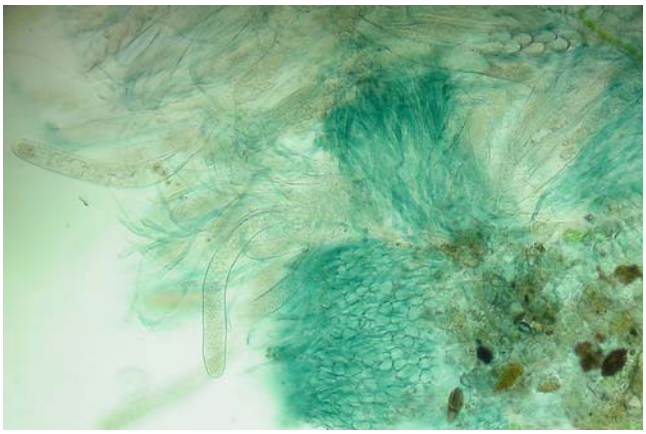

Figure 25. ***Calypogeia azurea*** with fungal parasite ***Mniaecia jungermanniae*** asci in the upper right corner of the image. Photo by Walter Obermayer, with permission.

Figure 26. ***Calypogeia azurea*** with asci of the fungal parasite ***Mniaecia jungermanniae***. Photo by Walter Obermayer, with permission.

Biochemistry

A number of studies have examined the secondary compounds in ***Calypogeia azurea*** (Figure 20-Figure 21). Among these, Nakagawara *et al*. (1992) looked at the azulenes in their study of sesquiterpenoids. One of these azulenes exhibits anti-inflammatory and anti-ulcer activity. Tazaki *et al*. (1998) likewise isolated a new sesquiterpenoid from the species.

Calypogeia fissa (Figure 27-Figure 29, Figure 33-Figure 34)

Distribution

Calypogeia fissa (Figure 27-Figure 29, Figure 33-Figure 34) has a suboceanic distribution pattern in North America, Europe, Asia, and North Africa (Potemkin 2018).

Figure 27. ***Calypogeia fissa***, a species with a suboceanic distribution in the Northern Hemisphere, occurring in a variety of wet habitats. Photo by Hermann Schachner, through Creative Commons.

Figure 28. ***Calypogeia fissa***. Photo by Štěpán Koval, with permission.

Figure 29. ***Calypogeia fissa*** ventral side showing under leaves. Photo by Michael Lüth, with permission.

Aquatic and Wet Habitats

Watson (1919) attributed this species to peaty ground, associated with fast water. Clapham (1940) reported it from the sides and tops of tussocks in calcareous fens in the Oxford District, UK. Its occurrence in the River Tweed, UK, was not common (Holmes & Whitton 1975a). It can occur in irrigation ditches (Beaucourt *et al*. 1987). In southern Finland it occurs in small lakes (Toivonen & Huttunen 1995). ***Calypogeia fissa*** (Figure 27-Figure 29, Figure 33-Figure 34) in the study area in northwestern European Russia grows on more or less wet humus as well as sandy soils and rotten wood near temporary water courses in coastal communities (Potemkin 2018). It also occurs in rock crevices with seepage where one might also find ***Scapania nemorea*** (Figure 30). ***Calypogeia fissa*** frequently forms rather extensive mats resulting from frequent production of gemmae (Figure 33) and probably regular spore production (Figure 34).

Figure 30. ***Scapania nemorea***, a species that can occur in rock crevices with ***Calypogeia fissa***. Photo by Michael Lüth, with permission.

Genetic and Physiological Differences

Buczkowska *et al.* (2011) identified two morphologically distinct groups of the ***Calypogeia fissa*** (Figure 27-Figure 29, Figure 33-Figure 34) complex in Europe. These were supported by statistical analysis of 34 morphological characters as well as by genetic distance. Furthermore, PCR indicates that the European and North American populations represent two subspecies of ***Calypogeia fissa*** (Buczkowska *et al*. 2012a): ***Calypogeia fissa*** subsp. ***fissa*** (Figure 31) in Europe and ***C. fissa*** subsp. ***neogaea*** (Figure 32) in North America (Buczkowska *et al*. 2015). These could be distinguished by both genetic and molecular markers. In Europe, there is a haploid group and a diploid group, with an isozyme pattern that suggests an **allopolyploid** (having two haploid sets of chromosomes that are dissimilar and derived from different species; *i.e.*, a hybrid which has a functional set of chromosomes from each parent of two species) origin of the diploid group. Such differences can express themselves in physiological differences without necessarily showing morphological differences. This can account for finding the species in different habitats on different continents.

Figure 31. ***Calypogeia fissa*** subsp. ***fissa***, the subspecies typical in Europe, showing underleaves. Photo by Hermann Schachner, through Creative Commons.

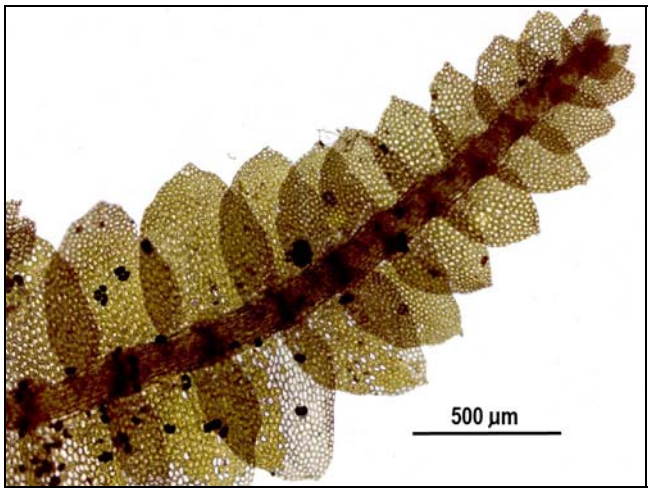

Figure 32. ***Calypogeia fissa*** subsp. ***neogaea***, the subspecies typical in North America; ventral leaves in the photo are the darkened areas across the stem.. Photo by Blanka Aguero, with permission.

Reproduction

Calypogeia fissa frequently forms rather extensive **mats** resulting from frequent production of gemmae (Figure 33) and probably regular spore production (Figure 34) (Schuster 1969; Potemkin 2018). ***Calypogeia fissa*** (Figure 27-Figure 29, Figure 33-Figure 34) is **autoicous** or **paroicous** (Schuster 1969).

Figure 33. ***Calypogeia fissa*** with gemmae. Photo by Štěpán Koval, with permission.

Figure 34. ***Calypogeia fissa*** with nearly mature capsule. Photo by Malcolm Storey, through Creative Commons.

It is able to regenerate from peat slabs (Duckett & Clymo 1988). Unlike some leafy liverworts, ***Calypogeia fissa*** lacks underground shoots (Figure 29). Therefore, it regenerates most abundantly at the surface, failing to have regenerative parts below 9 cm depth in the peat.

Fungal Interaction

Wang and Qiu (2006) found a report of fungal association with ***Calypogeia fissa*** (Figure 27-Figure 29, Figure 33-Figure 34), but I have not found details of this record.

Biochemistry

Warmers and König (1999) found four new sesquiterpenes in ***Calypogeia fissa*** (Figure 27-Figure 29, Figure 33-Figure 34). Their role remains unknown, but they are likely to play a role in antiherbivory. The oil bodies (Figure 35) typically house such secondary compounds.

Figure 35. ***Calypogeia fissa*** leaf cells showing colorless oil bodies. Photo by Hermann Schachner, through Creative Commons.

Calypogeia goebelii (Figure 36)

(syn. = *Kantia goebelii* fo. *thermarum*)

Distribution

Calypogeia goebelii (Figure 36) is distributed in Australia, Oceania, and southern Asia (Guala & Döring 2019).

Figure 36. ***Calypogeia goebelii***, a species that lives in thermal acidic sprays, from Australia, Oceania, and southern Asia. Photo through Creative Commons.

Aquatic and Wet Habitats

Ruttner (1955) reported this species from areas with thermal acidic spray in the tropics. Elsewhere, Kitagawa (1978b) reported ***Calypogeia goebelii*** (Figure 36) from 1550-1600 m asl in the evergreen forest of Thailand as terrestrial and listed its distribution as Java, Sumatra, New Guinea, and Micronesia.

Calypogeia muelleriana (Figure 37-Figure 40)

Like many of the liverworts, the taxonomy has been confusing for ***Calypogeia muelleriana*** (Figure 37-Figure 40). Buczkowska (2010) found that among 52 samples from Poland that resembled ***Calypogeia muelleriana***, 21 belonged to a new taxon, as identified with isozyme markers. Based on Chloroplast DNA sequences, this new taxon more closely resembles ***C. azurea*** (Figure 20-Figure 21) than it does ***C. muelleriana*** and this unnamed new species has also been identified in the USA (Buczkowska *et al*. 2013)

Distribution

Calypogeia muelleriana (Figure 37-Figure 40) is widespread in Europe, but was poorly known in North America (Stotler & Vitt 1972). It is circumpolar and bipolar (Emerson & Loring 2010). Hong (1990) added a number of locations in western USA and Canada, including shaded decaying logs, moist loam, and shaded damp stream banks. He described two new forms (fo. ***schofieldii*** and fo. ***shieldsii***) in this western North American region. It is also known in eastern North America from Manitoulin Island, Ontario, Canada (Williams & Cain 1959), in North and South Carolina, USA (Raczka 2014), and in Pickle Springs, Missouri, USA (Stotler & Vitt 1972).

Figure 37. ***Calypogeia muelleriana***, a species widespread in Europe on stream and river banks and in lakes. Photo by Hermann Schachner, through Creative Commons.

Aquatic and Wet Habitats

In the Pickle Springs, Missouri, USA, ***Calypogeia muelleriana*** (Figure 37-Figure 40) occurred on sandy soil of stream banks (Stotler & Vitt 1972) and in North and South Carolina, USA, along the Waccamaw River (Raczka 2014). Leclercq (1977) also reported it from earthy and gravelly substrates of river banks in Haute Ardenne rivers, Belgium. In Germany, it occurs in upper and middle

stream reaches in the Harz Mountains (Bley 1987). In southern Finland it occurs in small lakes (Toivonen & Huttunen 1995). These latter two suggest that it is facultatively aquatic.

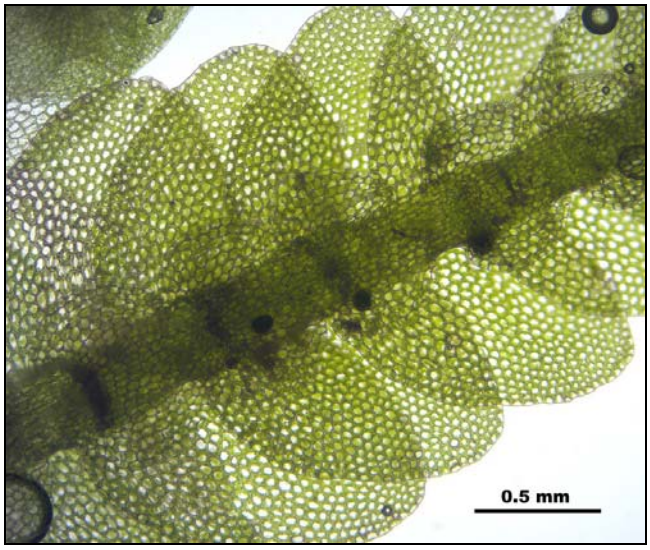

Figure 38. ***Calypogeia muelleriana*** ventral side with underleaves. Photo by Hermann Schachner, through Creative Commons.

Reproduction

Calypogeia muelleriana (Figure 37-Figure 40) is **monoicous**, with both male and female reproductive organs developing from short lateral branches (Schuster 1969). After fertilization, a spore-bearing capsule develops, splits, and releases spores to the wind. Sometimes gemmae develop near the tips of its leafy stems (Figure 39-Figure 42) or around the leaf margins. These gemmae eventually detach, after which they can form new clonal plants under favorable conditions.

Figure 39. ***Calypogeia muelleriana*** habitat showing plants with gemmae. Photo by Michael Lüth, with permission.

Figure 40. ***Calypogeia muelleriana*** with gemmae. Photo by David T. Holyoak, with permission.

Figure 41. ***Calypogeia muelleriana*** with terminal gemmae. Photo by Des Callaghan, with permission.

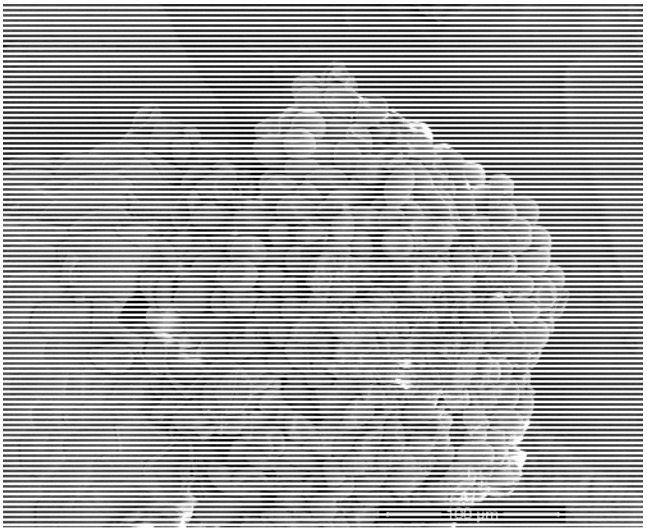

Figure 42. SEM of ***Calypogeia muelleriana*** leaf with gemmae. Photo by Jeff Duckett and Silvia Pressel. with permission.

Biochemistry

Some of its secondary compounds have been identified. Warmers *et al*. (1998) investigated the lipophilic constituents and reported three new sesquiterpene compounds. Such compounds often occur in the oil bodies (Figure 43).

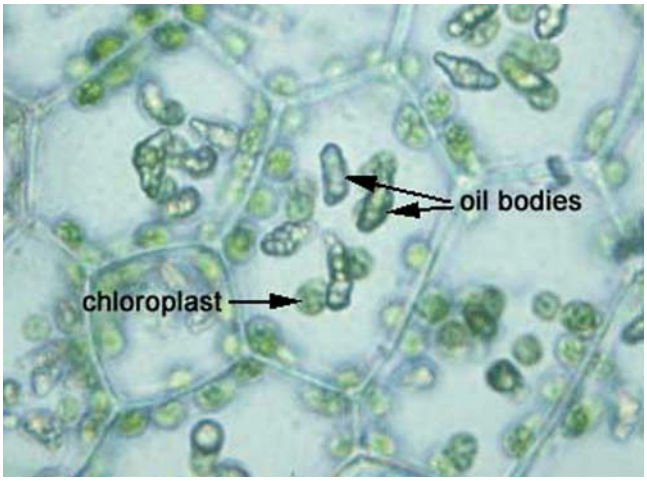

Figure 43. ***Calypogeia muelleriana*** showing oil bodies in leaf cells. Photo from Botany Website, UBC, with permission.

Calypogeia sphagnicola (Figure 44-Figure 46)

(syn. = *Calypogeia muelleriana* fo. *sphagnicola*)

Distribution

Calypogeia sphagnicola (Figure 44-Figure 46) is widely distributed, occurring in the subarctic and alpine areas in northern and central Europe, from Greenland southward, and North America, with a report from Japan (Schuster 1969). In North America it extends from Alaska southward to Alberta and British Columbia in the west and from Newfoundland (Weber 1976), Quebec, and Ontario to West Virginia in the east (Schuster 1969). In the southern extensions it is primarily in spruce and tamarack bogs – habitats that are often considered **refugia** (locations which support isolated or relict population of once more widespread species) and suggest it may have had a wider distribution at one time.

Aquatic and Wet Habitat

Of the many references I found documenting the presence of this species, all but one indicated it was associated with ***Sphagnum*** (Figure 46). Thus, I question the record from North Carolina, USA, indicating that it was found on moist soil (Blomquist 1936) and suggest it may have been a misidentification – or incomplete habitat information.

Figure 44. ***Calypogeia sphagnicola***, a species from sub-Arctic and alpine areas in the Northern Hemisphere. Photo by Erika Mitchell, through Creative Commons.

Figure 45. ***Calypogeia sphagnicola*** showing underleaf. Photo by Scot Loring, through Creative Commons.

Figure 46. ***Calypogeia sphagnicola*** with ***Sphagnum***. Photo by David T. Holyoak, with permission.

Calypogeia sphagnicola (Figure 44-Figure 46) has earned its name because it occurs almost exclusively in ***Sphagnum*** bogs, but also on ***Sphagnum***-capped crests of cliffs (Schuster 1969; Emerson & Loring 2010). ***Calypogeia sphagnicola*** occurs at the summits of ***Sphagnum*** hummocks in southern France (Hugonnot 2011). They are able to colonize degenerating mats in communities with other leafy liverworts. It is one of the species that has high conservation value because of its restriction to specific microhabitats, especially dying ***Sphagna***. Kitagawa (1978a) likewise reported this species from oligotrophic moors where it grows among ***Sphagna*** in the alpine zone of Ödake, Japan, but its primary distribution is in the Arctic, with only three locations in Japan in Japan's northern mountains. Near Gladkovskaya Bay in Russia, Bakalin (2005) found it to occur on the peaty banks of ponds in a peat moss-sedge mire, typically occurring with other liverworts. Bakalin *et al.* (2016) reported it from bare peat of peat moss tussocks in mires in the Putorana Plateau of eastern Siberia, where it grew with other liverworts.

Albisson (1997) considered ***Calypogeia sphagnicola*** (Figure 44-Figure 46) to have a somewhat wider ecological

amplitude than some of the mire specialists. They also found that these liverworts occur more frequently with ***Sphagnum*** species in subgenera ***Sphagnum*** (Figure 47) and ***Acutifolia*** Figure 48) than in subgenus ***Cuspidatum*** (Figure 49). This is consistent with the observations of Souto *et al*. (2015) who found that ***C. sphagnicola*** was associated with dense carpets of ***Sphagnum magellanicum*** (Figure 47), a moss in subgenus ***Sphagnum***.

Figure 47. ***Sphagnum magellanicum***, subgenus ***Sphagnum***, showing a dense carpet that can serve as substrate for ***Calypogeia sphagnicola***. Photo by Dale Vitt, with permission.

Despite its relative rarity, ***Calypogeia sphagnicola*** (Figure 44-Figure 46) is able to successfully compete with other liverworts by over-growing the ***Sphagnum*** capitula in the hummocks, but this is further supported by other liverworts that overgrow the ***Sphagnum*** and reduce its growth rate (Nordbakken 1996). Hugonnot *et al*. (2015) suggest that ***C. sphagnicola*** grows over actively growing ***Sphagnum*** capitula (Figure 46), whereas some leafy liverwort species avoid the ***Sphagnum*** competition by growing on bare peat as well as among ***Sphagnum***.

Figure 48. ***Sphagnum girgensohnii***, subgenus ***Acutifolia***, representing the more preferred substrate group for ***Calypogeia sphagnicola***. Photo by Kari Pihlaviita, through Creative Commons.

In the Alaskan black spruce forest, ***Calypogeia sphagnicola*** (Figure 44-Figure 46) forms small patches or even isolated shoots (Seppelt *et al*. 2008). These are green to pale green to yellowish-green, but older parts are frequently yellowish-brown.

Reproduction

Calypogeia sphagnicola (Figure 44-Figure 46) is **monoicous** (Schuster 1969). Gemmae are common (Bosanquet 2021).

Figure 49. ***Sphagnum cuspidatum*** (subgenus ***Cuspidatum***) submersed; this species prefers wetter habitats than most ***Sphagnum*** species and is not a preferred substrate for ***Calypogeia sphagnicola***. Photo by Bernd Haynold, through Creative Commons.

Biochemistry

Buczkowska *et al*. (2012b) used isozymes to determine that two forms of ***Calypogeia sphagnicola*** (fo. ***sphagnicola*** and fo. ***paludosa***) represent genetically distinct species. The former is haploid and the latter is diploid. They likewise differ distributionally in Poland. "***Calypogeia sphagnicola*** fo. ***sphagnicola*** occurs exclusively in the lowlands of the northern part of the country on raised peat bogs; ***C. sphagnicola*** fo. ***paludosa*** is found only in the mountains of southern Poland, mainly in the subalpine zone, where it grows on ***Sphagnum-Polytrichum*** hummocks (Figure 50) on the upper part of north-facing slopes."

Figure 50. ***Sphagnum capillifolium*** and ***Polytrichum commune*** forming a hummock where ***C. sphagnicola*** fo. ***paludosa*** is able to grow. Photo by Sheila, through Creative Commons.

Fungal Interactions

Wang and Qiu (2006) reported that ***Calypogeia sphagnicola*** (Figure 44-Figure 46) has fungi associated with it.

Calypogeia sullivantii (Figure 51)

Distribution

Calypogeia sullivantii (Figure 51) occurs from Maine to Florida and Puerto Rico and west to Ohio, Missouri, Mississippi, Kentucky, and Louisiana, all in the eastern half of the USA (Pagán 1939; Schuster 1969). In the eastern states, Schuster and Patterson (1957) considered it to be a mostly mountain species.

Figure 51. ***Calypogeia sullivantii***, a species previously considered a variety of ***C. arguta***, occurs around springs. Photo by Blanka Aguero, with permission.

Aquatic and Wet Habitats

Wittlake (1950) found that ***Calypogeia sullivantii*** (formerly placed in ***C. arguta*** as a variety; Figure 51) occurred around springs at Spy Rock Hollow, Arkansas, USA, in association with other mosses and liverworts. Guerke (1971) reported this species from moist ditch banks in Louisiana, USA. In West Virginia, it lives in a sandstone cave where there is a constant drip from the ceiling of the cave, along with seepage, that keeps the cave continuously wet (Ammons 1933). In southern Illinois, Skorepa (1968) found it on wet clay and rocks and under a sandstone ledge. Pagán (1939) found it on wet banks and on rocks in Puerto Rico.

But its habitat is not always wet. Vitt (1967) reported it from sandy soil in the forest above and below a cliff area at Pickle Springs, Missouri, USA. Fulford (1934) found it on moist, sandy soil in Kentucky, USA. Evans (1907) found that it usually grows scattered among other plants or in loose thin tufts. Schuster (1969) lists a variety of habitats, including stream banks, along cascading brooks, and on moist or damp soil in deep shade.

Reproduction

Calypogeia sullivantii (Figure 51) is **autoicous** (having separate male and female branches but on same plant) (Schuster 1969). They reproduce asexually by gemmae.

Geocalycaceae

Geocalyx graveolens (Figure 52-Figure 54)

Distribution

Geocalyx graveolens (Figure 52-Figure 54) is a widespread species in oceanic Holarctic regions (Szweykowski & Kozlicka 1974; Schäfer-Verwimp & Váňa 2011; Hugonnot 2014). In North America, it is abundant from Alaska to California and from Labrador to North Carolina and Tennessee (Hugonnot 2014). Nevertheless, it does not reach the tundra (Schuster 1980). It is much less common in Europe, and Asia exhibits only local occurrences.

Figure 52. ***Geocalyx graveolens***, a Holarctic species that extends southward into the mountains, occurring in such wet habitats as humus, peat, and mires. Photo by Hugues Tinguy, with permission.

Figure 53. ***Geocalyx graveolens*** ventral side showing underleaf at the red star. Photo by Michael Lüth, with permission.

Aquatic and Wet Habitats

Its most common habitats seem to be on humus, peaty soil, or decayed forest litter in mires, often on banks or sides of ledges (Simó *et al.* 1978; Schuster 1980; Damsholt 2002; Nebel & Philippi 2005). Gabriel and Bates (2005) considered it to be indicative of the wettest sites in the Azores.

In Germany ***Geocalyx graveolens*** (Figure 52-Figure 54) is very rare, occurring in calcareous alder breaks with "brisk" water (Rätzel *et al*. 2004). In western Canada, Vitt *et al*. (1986) found that it fell in the restricted terrestrial category when associated with montane streams. In eastern Canada, in Ontario, Cain and Fulford (1948) reported it from wet rotten logs, humus, and peat in deep shade, being very common throughout the province. Similarly, Evans and Nichols (1935) reported it on logs in swampy woods in the Upper Peninsula of Michigan, USA, and Steere (1934) likewise found it on rotten wood and humus in swamps and wet woods on Sugar Island, Michigan. Sharp (1944) made a similar habitat observation at Mountain Lake, Virginia, USA. Järvinen (1976) reported similar habitats in eastern Fennoscandia.

In the Himalayas, Long (2005) found it in mossy carpets under dripping cliffs. Several researchers have found it on the banks of brooks and rivers (*e.g.* Figure 54) (Plitt 1908 in Maryland, USA; Greenwood 1910 in Massachusetts, USA; Burnham 1919 in the Lake George area of New York, USA). In Massachusetts, these habitats also include damp soil on the edge of streams (Greenwood 1915). Darlington (1938) found it on moist ground near Glen Lake in Michigan, USA. Clee (1937) found it on shaded hedge banks that had an abundance of water. Mogensen and Damsholt (1981) found it in habitats with percolating water. Further attesting to its broad ecological amplitude, Váňa and Ignatov (1996) found it in the Altai Mountains in eastern Asia on a sand bar that was temporarily flooded in a stream running through a narrow canyon. Fulford (1934) found it growing over moist, shaded sandstone cliffs in Kentucky, USA. Ingerpuu *et al*. (2014) considered it to be a facultative fen species in Estonian mires.

Figure 54. ***Geocalyx graveolens*** on stream bank. Photo by Michael Lüth, with permission.

In contrast to these wet habitats, it occurs on sandstones in Baden Wurtemberg (Nebel & Philippi 2005) and Vosges (Frahm 2002) in the oriental Pyrenees (Hugonnot 2014). Furthermore, in North America (Schuster 1953) and Nordic countries (Damsholt 2002) ***Geocalyx graveolens*** (Figure 52-Figure 54) seems to tolerate subcalcareous situations, but this is not the case in the British Isles (Paton 1999). Zubel (2009) found that in southeastern Poland, it occurs on rock, sandstone, mineral soil, and humus in the mountains, but in the lowlands it occurs on rotting wood, humus, and tree bases in wet and very wet sites in alder forests and other wet forest types or boggy forests.

In North America, Schuster (1953) considered that the species showed a decided tolerance for subcalcareous conditions, and Damsholt (2002) for basic rocks in Nordic countries, which apparently is not the case in the British Isles (Paton, 1999).

Reproduction

Geocalyx graveolens (Figure 52-Figure 54) forms extensive creeping mats over ***Sphagnum*** species (Figure 47). Sharp (1944) described it as having a peculiar yellowish color (Figure 52). It typically produces numerous capsules. Ross-Davis and Frego (2004) found its diaspores in diaspore rain and buried propagule banks. Its rarity, particularly in Europe, would not seem to be caused by a limited number of suitable habitats or propagules.

Role

These mats can serve as home for the boreid beetle, ***Caurinus dectes*** (Figure 55), where the beetles feed on the liverwort on decaying logs (Russell 1979). Asakawa (1998) reported a turpentine-like odor in this liverwort species. It is possible that this odor discourages some of the potential insect herbivory, but it apparently has no negative effect on ***Caurinus dectes***.

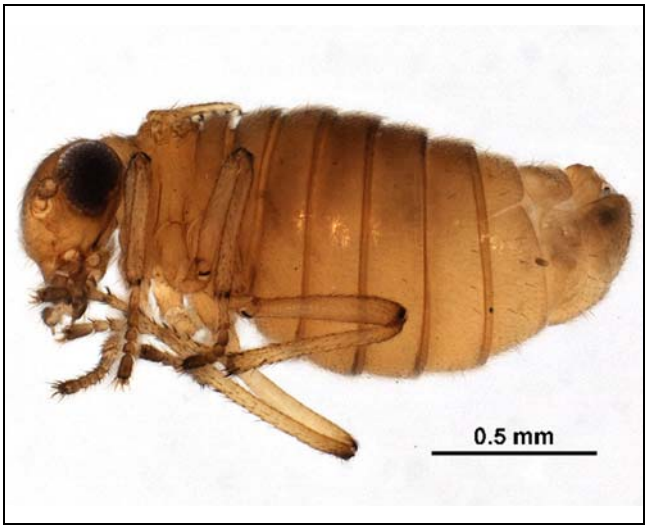

Figure 55. ***Caurinus dectes***, a boreid beetle that feeds on ***Geocalyx graveolens***. Photo by CBG Photography Group, through Creative Commons.

Fungal Interactions

In their study on liverwort-fungal symbioses, Bidartondo and Duckett (2010) were only able to find **Ascomycetes**. This was different from the previous reports of **Basidiomycetes** on this species.

Gymnomitriaceae

Gymnomitrion commutatum (Figure 56)

(syn. = *Marsupella commutata*)

Distribution

Gymnomitrion commutatum (Figure 56) occurs in Europe, Siberia, Russian Far East, China, eastern Asia, Indian Subcontinent, Malesia, subarctic America, western Canada, northwestern USA (Váňa *et al*. 2010), Iceland, and South Greenland (Konstantinova 2000).

Figure 56. ***Gymnomitrion commutatum***, a Northern Hemisphere wet habitat liverwort. Photo by Michael Lüth, with permission.

Aquatic and Wet Habitats

Konstantinova *et al*. (2002) found ***Gymnomitrion commutatum*** (Figure 56) on wet cliffs and cliff crevices associated with the Upper Bureya River in the Russian Far East. Bakalin (2008) found it on cliffs near streams in the tundra belt in several locations in the Sakhalin Province, Russia. Choi *et al*. (2013) found it at elevations of 1400-1614 m asl in Mt. Deogyu National Park in the Republic of Korea, where it occurred on shaded cliffs and rocks. Its records are few, and it is included in the Red Data Book for Russia (Sofronova *et al*. 2015). ***Marsupella commutata*** grows on crystalline substrates in streams on the Ushkovskii Volcano, Kamchatka (Bakalin 2006).

Adaptations

This high altitude species is blackish-brown (Mamontov *et al*. 2018), a characteristic that most likely protects it from the high levels of UV radiation at those altitudes.

Reproduction

Gymnomitrion commutatum is only occasionally fertile and capsules are rare in the UK (Smith 1990).

Gymnomitrion crenulatum (Figure 57-Figure 58)

Distribution

The distribution of ***Gymnomitrion crenulatum*** (Figure 57-Figure 58) is in question because of misidentifications. Váňa *et al*. (2010) consider it confined to northern and southwestern Europe, with other locations representing misidentifications. However, GBIF (2020c) still includes Norway, Finland, Britain, Ireland, France, Portugal, Spain, Yamal-Nenets, Tibet (Xizang), Sichuan, Yunnan, Japan, Alaska, Nunavut, British Columbia, Washington, and South Georgia.

Figure 57. ***Gymnomitrion crenulatum***, a Northern Hemisphere species with a poorly understood distribution; it seems to prefer emergent rocks of streams, but can get submersed. Photo by Andrew Hodgson, with permission.

Aquatic and Wet Habitats

This species seems to do best above the low flow water level in exposed streambed conditions, preferring moderately stable boulders (Figure 58) that are easily submerged (Vieira *et al*. 2005). It is tolerant of acid water, perhaps preferring it, especially in mountain streams of northwest Portugal. Casas *et al*. (1999) reported it on rocks by a stream in shrubby heathland in Spain.

Figure 58. ***Gymnomitrion crenulatum*** habitat in rock crevices. Photo by Andrew Hodgson, with permission.

One of the populations studied was reduced considerably by a strong fire, causing rock sediments to erode the bryophyte communities in the streambed (Vieira *et al*. 2004). In more protected locations it typically forms dense patches.

Reproduction

When Rawat *et al*. (2016) reported ***Gymnomitrion crenulatum*** (Figure 57-Figure 58) from India for the first time, they reported that they found no fertile plants. Its rarity most likely contributes to lack of observations on reproduction, but conversely, the rarity of reproduction probably contributes to the rarity of plants. In the UK, the plant is only occasionally fertile and capsules are very rare (Smith 1990).

Marsupella (Figure 59-Figure 62, Figure 63-Figure 67, Figure 70-Figure 87, Figure 89)

Marsupella (Figure 59-Figure 62, Figure 63-Figure 67, Figure 70-Figure 87, Figure 89) has more than one species in aquatic habitats, and these have at times been registered as the genus only. These include a dominance in the upper and middle reaches in the Harz Mountains of Germany (Bley 1987) and occurrence in small, pristine streams of the Tolvajärvi region, Russian Karelia (Vuori *et al*. 1999).

Marsupella aquatica (Figure 59-Figure 62)

(syn. = *Marsupella emarginata* var. *aquatica*)

Marsupella aquatica (Figure 59-Figure 62) seems to be confined to alpine or subalpine regions (Evans 1904). ***Marsupella emarginata***, on the other hand, extends downward into the plains, at least in eastern North America.

Distribution

Marsupella aquatica (Figure 59-Figure 62) has an **arctomontane** (in Arctic and in montane regions at lower latitudes) semi-circumpolar distribution with oceanic affinities (Konstantinova 2000). More specifically, Váňa *et al*. (2010) list it for northern and southwestern Europe, Asia, including Macaronesia, Siberia, Russian Far East, Caucasus, subarctic America, Canada, and northwestern and northeastern USA. They consider other records in North America to be misidentifications.

Figure 59. ***Marsupella aquatica***, an Arctic-montane semi-circumpolar species from wet and submerged rocks of streams and rivers. Photo by Štěpán Koval, with permission.

Aquatic and Wet Habitats

Nichols (1918) reported ***Marsupella aquatica*** (Figure 59-Figure 62) from ravines on Cape Breton Island, Canada. Lorenz (1924) reported it on rocks in Deer Brook on Mt. Desert, Maine, whereas the more western species ***M. emarginata*** (Figure 65-Figure 66) was frequent on wet rocks. Watson (1919) considered ***Marsupella aquatica*** to be a species that grows submerged in slow water with poor mineral salts and to occupy more aquatic rocks than ***Marsupella emarginata***. Dulin *et al*. (2009) likewise reported ***M. aquatica*** from streams with poor mineral salts in the Vologda Region of Russia, where it frequently occurred with ***Scapania undulata*** (Figure 60) and ***Fontinalis dalecarlica*** (Figure 61). Koppe (1945) reported it from stones in streams in the Westfalens of northwestern Germany. Koponen *et al*. (1995) merely listed it as aquatic in Finland. Vieira *et al*. (2005) reported it from mountain streams in northwest Portugal. By contrast, Lepp (2012) reported that it occurs to depths of 30 m in Australia, and Heggenes and Saltveit (2002) reported that it forms a carpet down to almost 40 m in the regulated River Suldalslågen in western Norway. This lake in the river is free of ice only from July to October.

Figure 60. ***Scapania undulata***, a species that associates with ***Marsupella aquatica*** on rocks in Maine, USA. Photo by Jan-Peter Frahm, with permission.

Figure 61. ***Fontinalis dalecarlica***, a species that associates with ***Marsupella aquatica*** on rocks in Maine, USA. Photo by J. C. Schou, with permission.

Bodin and Nauwerk (1968) studied the biology of the leafy liverwort ***Marsupella aquatica*** (Figure 59-Figure 62), the dominant member of the well-developed bryophyte vegetation of Latnajaure, a mountain lake (maximum depth 43.5 m) in the Abisko area of Sweden. ***Marsupella aquatica*** increases in size and robustness with depth in Latnjajaure in Swedish Lappland.

Monteith (1996) reported that ***Scapania undulata*** (Figure 60) may be replacing ***Marsupella aquatica*** (Figure 59-Figure 62), a common inhabitant in acid streams, following an experimental burn.

Adaptations

Marsupella aquatica can reach 10 cm long and is dark green to almost black, not red-brown (Smith 1990; Wagner 2008). In contrast to Wagner, Evans (1904) describes the color as bright green to reddish. The latter dark coloration can protect it from the high UV radiation in its alpine habitat. The stems branch little and are very firm (Evans 1904). A cross-sectional view reveals that stem cells are all about the same size. Those in the middle have thin walls, grading to thicker walls toward the outer cells. The outermost layer has shorter cells than the interior.

Figure 62. ***Marsupella aquatica***, exhibiting a red form. Photo by Barry Stewart, with permission.

Reproduction

Marsupella emarginata is **dioicous** (Smith 1990).

Biochemistry

Marsupella aquatica (Figure 59-Figure 62) has received less biochemical attention than some of the previously mentioned bryophytes. Huneck *et al*. (1982) identified an Ent-longipinane derivative from the species. Nagashima *et al*. (1994) identified a new gymnomitrane-type sesquiterpenoid from it, as well as others that were previously known. Adio *et al*. (2002) identified volatile compounds from ***Marsupella aquatica***. Leong *et al*. (2002) identified amorphane sesquiterpenoids from the species in Scotland. Later Adio *et al*. (2007) determined nine amorphane sesquiterpenoid constituents of the species from Austria.

Marsupella boeckii (Figure 63)

Distribution

Marsupella boeckii (Figure 63) occurs in the Antarctic-Southern Ocean area, Europe, including Svalbard (Konstantinova & Savchenko 2008), Asia, and North America from Alaska to continental USA (ITIS 2020a).

Figure 63. ***Marsupella boeckii***, a species of scattered locations worldwide, occurring in wet habitats such as the edges of springs and wet cliffs. Photo from Earth.com, with permission.

Aquatic and Wet Habitats

Koponen *et al*. (1995) reported it as aquatic in Finland. Konstantinova and Savchenko (2008) found it in Svalbard at the edge of a spring that was covered with mats of ***Marsupella arctica*** (Figure 64) where both occurred on shallow sandy soil (<1 cm) overlying rocks. Sofronova (2018) found that it created "minute" cover up to 1 cm square on wet cliffs, compared to carpets of more than 1 sq m of ***Marsupella emarginata*** (Figure 65-Figure 67) in the same habitat in eastern Yakutia, Russia.

Figure 64. ***Marsupella arctica*** herbarium specimen, a species that forms mats at the edges of springs. Photo by CBG Photography Group, through Creative Commons.

Reproduction

Marsupella boeckii is **dioicous** (Smith 1990; Konstantinova & Savchenko 2008).

Marsupella emarginata (Figure 65-Figure 67)

(syn. = *Nardia emarginata*)

Distribution

Marsupella emarginata (Figure 65-Figure 67) is a widespread Laurasian species that extends into the tropics in the high mountains (Váňa 1993). It occurs in Europe, Asia, North America from Alaska to Mexico, South America (ITIS 2020b), and Africa (Váňa 1993).

Figure 65. ***Marsupella emarginata***, a widespread Northern Hemisphere species that extends into the high mountains of the tropics where it is common in streams and rivers and banks. Photo by Michael Lüth, with permission.

Aquatic and Wet Habitats

Marsupella emarginata (Figure 65-Figure 67) is the most common species in the genus, as noted by Scarlett and O'Hare (2006), in English and Welsh rivers. It is common and abundant in wet or damp acidic places, especially on rocks or gravel both in and beside streams and rivers. Its less wet habitats include humid woodland rocks in woods, wet crags, lake margins, wet gravel tracks, and near snowbeds. Sofronova (2018) similarly found it in places of late snow melt in East Yakutia, Russia. It often occurs in mountain streams (Vieira *et al*. 2005 – northwest Portugal; Knapp & Lowe 2009 – Great Smoky Mountains National Park, Kentucky, USA; Luis *et al*. 2015 – Madeira Island).

Figure 66. ***Marsupella emarginata*** in its green form, showing mat growth. Photo by Barry Stewart, with permission.

West (1910) reported this species from wet rocks and shores, often submersed, in Scotland. In Connecticut, USA, it occurs on wet or moist cliffs of ravines, but it is calciphobic along rivers (Nichols 1916). On Cape Breton Island, Canada, Nichols (1918) found it again on rocks of a ravine stream bank and on wet rock cliffs associated with streams. Sofronova (2018) found it on wet cliff habitats in carpets of more than 1 sq. m. Watson (1919) attributed its most common occurrence to rocks in fast water, on banks with frequent submergence in slow water that is low in mineral salts, in waterfalls, and on mostly submerged rocks in fast streams. Weber (1976) likewise found it in Newfoundland, Canada, in the narrow zone that is periodically submerged along the river (Figure 67).

Figure 67. ***Marsupella emarginata*** in its habitat, forming mats on a bank where it can be periodically submerged. Photo by Chris Wagner, through Creative Commons.

It also occurs in European springs, particularly in the Central Alps (Zechmeister & Mucina 1994). In the Altai Mountains, Váňa and Ignatov (1996) found it on wet rocks of deep canyons and near a waterfall in the lower forest zone, but also in the alpine zone among rocks in rock fields, and in the subalpine covering wet cliffs with extensive pure mats.

Koponen *et al*. (1995) considered it to be an aquatic species in Finland. Ferreira *et al*. (2008) reported it as growing in rivers. Szweykowski (1951) considered it to be an acidophile (*p*H 4.0-6.0) in streams of Gory Stolowe Mountains, Poland, terming it a **hydroamphibiont** in streams. Thiébaut *et al*. (1998) considered it to be an acidophilous stream species in the Vosges Mountains of northeastern France, being sensitive to high ion concentrations. Geissler (1975, 1976) termed it a **helokrene** (living in marsh spring communities) in European alpine areas. Vanderpoorten and Klein (1999a) found that it could tolerate neutral *p*H if it is in **oligomineral** (having few dissolved minerals) waters; sewage effluent causes populations to decrease. Light (1975) reported it from small lakes in the Scottish mountains, where it experienced ice cover 4-7 months of the year; again, it preferred low ion concentrations. Satake *et al*. (1989) reported in from the acid river Akagawa, Japan. Tremp and Kohler (1991) likewise reported it as

submersed in low-buffered streams and Bahuguna *et al*. (2013) reported that it grows only in water low in solutes. Kohler and Tremp (1996) found ***Marsupella emarginata*** (Figure 65-Figure 67) to be an indicator of silicate rock areas with acidic water. Birk and Willby (2010) likewise found it to be somewhat common in siliceous mountain streams. In view of these low-ion occurrences, Tremp 2003) classified the species as **oligotrophic** (preferring low nutrients). Vanderpoorten (2012) considered it to be an indicator species for acidic waters with low buffering capacity.

In West Virginia, USA, ***Marsupella emarginata*** (Figure 65-Figure 67) preferred a *p*H of around 4.17 in mountain streams (Stephenson *et al*. 1995). In the Haute Ardenne rivers of Belgium, it is known from earthy and gravelly substrates of river banks (Leclercq 1977). But it also occurs near water on the wall of the Flume at Franconia Notch, New Hampshire, USA (Glime 1982). In the Canary Islands, it is never dominant and occurs on moist, shaded, soft volcanic rocks of the laurel forest (Dirkse 1985). Wagner *et al*. (2000) reported it from 40 and 70 m depth in Waldo Lake, Oregon, USA.

It occurs in association with ***Scapania undulata*** (Figure 60) in aquatic habitats of eastern Odenwald and southern Spessart (Philippi 1987) and in the ***Platyhypnidium*** (Figure 68)***-Fontinalis antipyretica*** (Figure 69) association in Thuringia, Germany (Marstaller 1987).

Figure 68. ***Platyhypnidium riparioides***, a species that can occur in association with ***Marsupella emarginata***. Photo by Hermann Schachner, through Creative Commons.

Figure 69. ***Fontinalis antipyretica*** in dried out small pool, a species that can occur in association with ***Marsupella emarginata***. Photo by Matt Goff, with permission.

Janauer and Dokulil (2006) report that when the water flow is too fast or runoff is too irregular, tracheophytic macrophytes are unable to become established, but bryophytes can become dominant. ***Marsupella emarginata*** (Figure 65-Figure 67) is one of those bryophytes to take advantage of these conditions (Lottausch *et al*. 1980).

In the River Dee, Maitland (1985) found dense liverwort growth, ***Marsupella emarginata*** (Figure 65-Figure 67) on most rock surfaces, reaching about 3 m diameter, but only 20 cm in depth (*e.g.* Figure 67).

Adaptations

Thiebaut *et al*. (1998) considered ***Marsupella emarginata*** (Figure 65-Figure 67) to be acidophilous and sensitive to high concentrations of cations. It disappears when Mg is too high and *p*H reaches 7.0. But they found that it was the cation concentration, not the *p*H that discouraged its presence. They concluded that it must have a physiological mechanism to regulate the difference in H^+ concentration between the cell and the surrounding water. They suggested that cations such as Mg and Ca limit the penetration of other elements needed by the plant cells.

Marsupella emarginata varies from bright green to reddish (Evans 1904). Reddish colors can help to protect the plants from damage by UV rays, particularly at high elevations, whereas green colors are more typical of bryophytes growing at lower light levels and lower elevations.

Reproduction

Marsupella emarginata (Figure 65-Figure 67) is **dioicous** with only occasional capsules that appear in late winter or spring in the UK (Smith 1990).

Fungal Interactions

Wang and Qiu (2006) report ***Marsupella emarginata*** (Figure 65-Figure 67) as having associations with fungi, but with no mycorrhizal relationships known. Egertová *et al*. (2016) found ***Mniaecia jungermanniae*** (Figure 24-Figure 26) in three samples of this species. Hopefully studies like that of Adio and König (2007) on sesquiterpenoids and other terpenes will help us to understand why some species have fungal partners or parasites and others do not.

***Marsupella emarginata* subsp. *tubulosa* (Figure 70)**

(syn. = *Marsupella tubulosa*)

Distribution

Marsupella emarginata* subsp. *tubulosa (Figure 70) has been identified in several studies. It is a subspecies of the Northern Hemisphere, primarily in eastern Asia and nearby islands, but also reported from fewer known locations in Europe and North America (GBIF 2020d). However, in their revision of the **Gymnomitriaceae**, Bakalin *et al*. (2021) exclude it from these latter areas and from the Russian far East continental mainland as incorrect identifications, based on the absence of the biconcentric character of the oil bodies there, confining it to the insular and peninsular areas in Amphi-Pacific Boreal and Temperate Eastern Asia

Aquatic and Wet Habitats

Bakalin *et al*. (2021) considered ***Marsupella emarginata*** subsp. ***tubulosa*** (Figure 70) to be acidophilic and meso- to hygrophytic. The species occupies sandy soils and mineral substrates, over wet to moist, and sometimes mesic cliffs, being most common along streams near running water in the Korean Peninsula. Song and Yamada (2006) reported it from wet rocks on Jeju (Cheju) Island, Korea. It occurs on a soil bank of a small creek of the Upper Bureya River in the Russian Far East (Konstantinova *et al*. 2002). On Mts. Hakkôda in northern Japan, it occurs on moist rocks (Kitagawa 1978a). Records of this subspecies with habitat data are harder to find despite its recorded number of locations.

Figure 70. ***Marsupella emarginata*** subsp. ***tubulosa*** forming mats in a small creek. Photo from Taiwan Mosses, through Creative Commons.

Biochemistry

Despite the paucity of readily available ecological information, Matsuo *et al*. (1979) isolated three new sesquiterpenoids from this species.

Marsupella koreana (Figure 71-Figure 73)

Distribution

Marsupella koreana (Figure 71-Figure 73) is probably an endemic species of the montane-temperate (Bakalin *et al*. 2021) Korean Peninsula, but is quite common there and has a highly variable morphology (Bakalin *et al*. 2019b). As a result, it may occur elsewhere, hiding under different names.

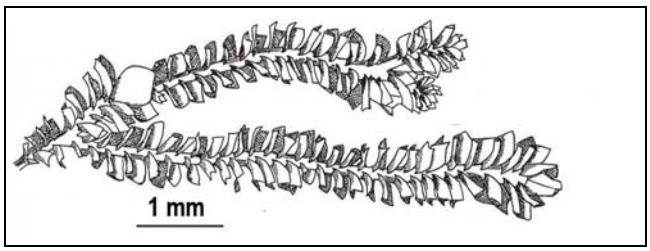

Figure 71. ***Marsupella koreana***. Drawing modified from Bakalin *et al*. 2021.

Figure 72. ***Marsupella koreana***, an apparent endemic of the Korean Peninsula. Photo modified from Bakalin *et al*. 2019; permission pending.

Figure 73. ***Marsupella koreana***. Photo modified from Bakalin *et al*. 2019;, permission pending.

Aquatic and Wet Habitats

Bakalin *et al*. (2019b) consider ***Marsupella koreana*** (Figure 71-Figure 73) to be acidophilic to neutro-tolerant and meso- to hygrophytic. It occupies mesic, rarer moist or dry substrata in open to partly shaded places.

Adaptations

The brownish green to deep green coloration of ***Marsupella koreana*** (Figure 71-Figure 73) (Bakalin *et al*. 2019b) suggest an adaptation to high light intensity. They form loose mats that are somewhat rigid (Bakalin *et al*. 2021). They have few or no rhizoids, but rhizoids are

common on geotropic stolons, a feature that should aid in their spread locally. Stems have hyaline epidermal cell with thick inner walls (Figure 74).

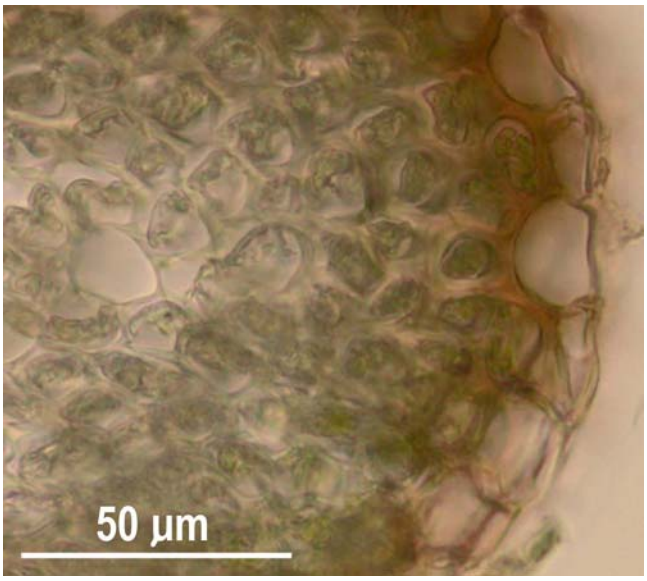

Figure 74. ***Marsupella koreana*** stem cross section showing thick inner walls of epidermal cells. Photo modified from Bakalin *et al.* 2019; permission pending.

Reproduction

Marsupella koreana (Figure 71-Figure 73) is **dioicous** (Bakalin *et al*. 2019b). Its spores are small (10-11 µm) and papillose.

Biochemistry

This rare endemic lacks biochemical studies, and it is not clear if it has oil bodies (Figure 75).

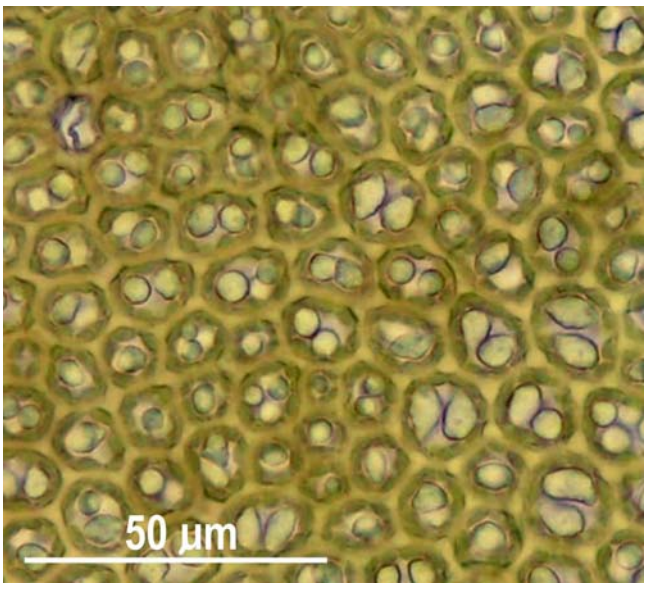

Figure 75. ***Marsupella koreana*** leaf cells with oil bodies? Photo modified from Bakalin *et al*. 2019; permission pending.

Marsupella pseudofunckii (Figure 76-Figure 77)

Distribution

Marsupella pseudofunckii (Figure 76-Figure 77) is a Temperate Montane East Asian species, known from Korea, China, Taiwan, the Russian Far East, and Japan (Bakalin *et al*. 2021).

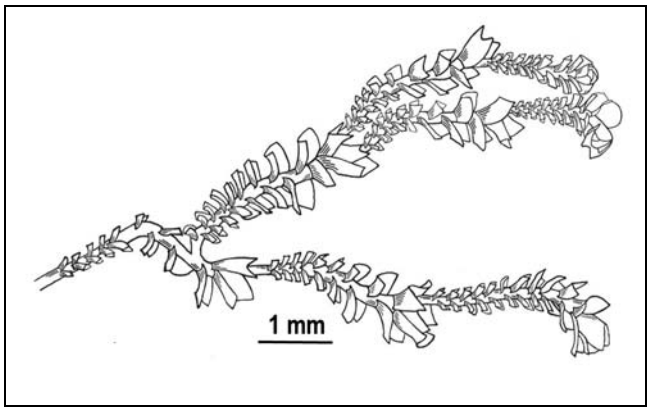

Figure 76. ***Marsupella pseudofunckii*** female plant. Drawing modified from Bakalin *et al.* 2021.

Figure 77. ***Marsupella pseudofunckii***. Photo from Bakalin *et al*. 2019; permission pending.

Aquatic and Wet Habitats

Marsupella pseudofunckii (Figure 76-Figure 77) is acidophilic and occurs as a mesophyte to hygrophyte (Bakalin *et al*. 2021). It occurs on dry to moist cliffs, rarely on wet rocks or stones near streams, in open or, more commonly, partly shaded places. Choi *et al*. (2013) list cliffs along streams, sometimes accompanied by ***Scapania undulata*** (Figure 60).

Adaptations

The species can at least sometimes form mats (Figure 78). These should help it to conserve water when it is not in a wet location. Its leaves also fold, further conserving water.

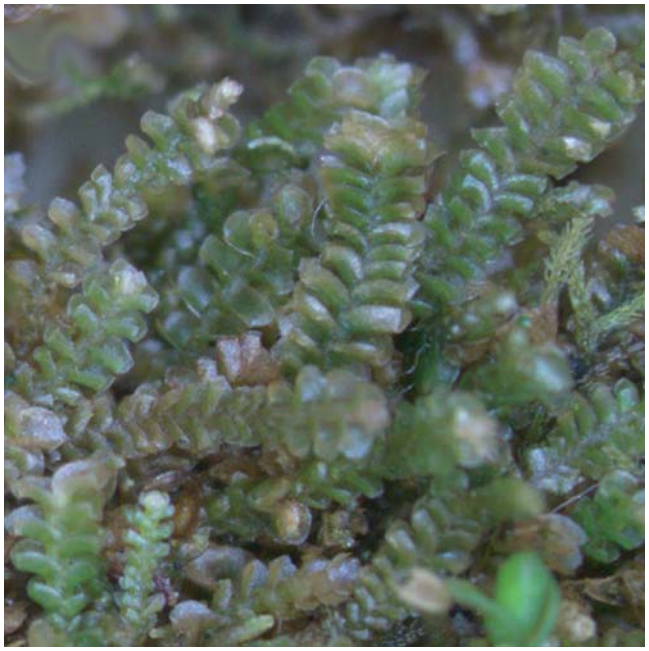

Figure 78. ***Marsupella pseudofunckii***, a montane east Asian species. Photo from Bakalin *et al*. 2019; permission pending.

Reproduction

Marsupella pseudofunckii (Figure 76-Figure 78) is **dioicous** (Bakalin *et al*. 2021).

Biochemistry

There seems to be nothing published on biochemistry of ***Marsupella pseudofunckii*** (Figure 76-Figure 78), and the oil bodies (Figure 79) are not described.

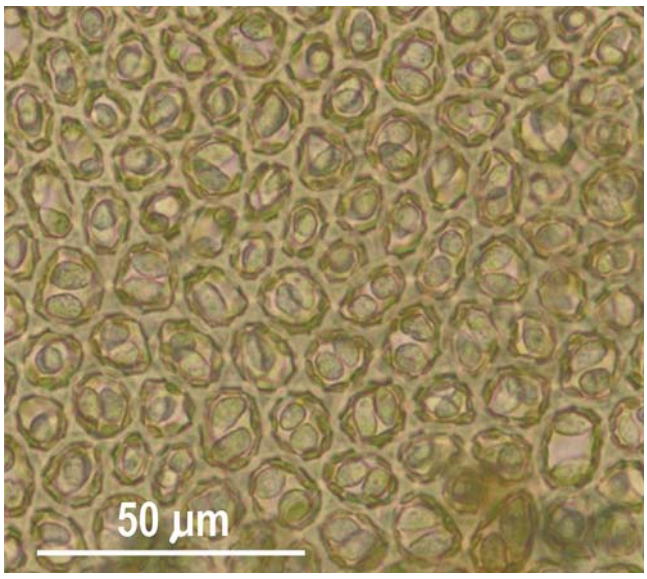

Figure 79. ***Marsupella pseudofunckii*** cells with oil bodies? Photo modified from Bakalin *et al*. 2019; permission pending.

Marsupella sparsifolia (Figure 80-Figure 81)

Distribution

Marsupella sparsifolia (Figure 80-Figure 81) is a bipolar species, mostly from Arctic-alpine and high subarctic areas (Schuster 1974). It occurs in Europe from Greenland and Scandinavia south to Great Britain and alpine central Europe. It also occurs in Uganda and the Cape of Good Hope, South Africa. In North America it occurs in the mountains of British Columbia and Alberta, Quebec, Canada, and in the USA on Mt. Washington, New Hampshire and in the Huron Mtns, Michigan. It also occurs in New Zealand.

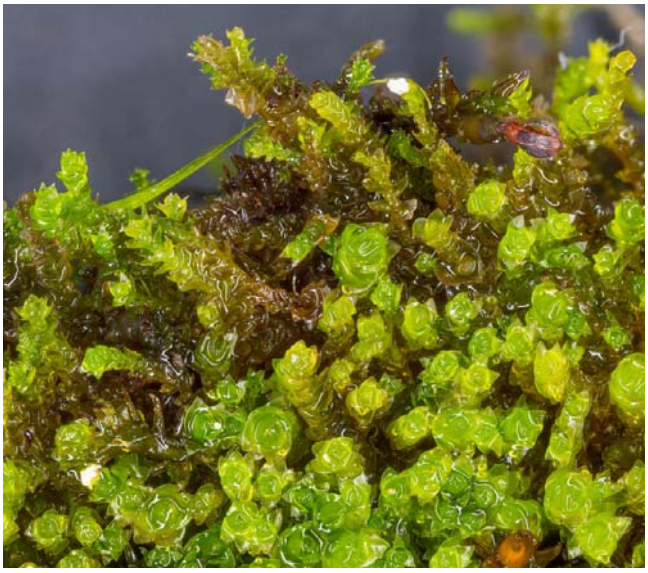

Figure 80. ***Marsupella sparsifolia*** in a wet habitat. Photo by Kristian Peters (Kersey Online; Sage bud), with permission.

Figure 81. ***Marsupella sparsifolia,*** is a bipolar Arctic-alpine species that occurs on stream banks and other wet habitats. Photo by Kristian Peters (Kersey Online; Sagebud), with permission.

Aquatic and Wet Habitats

Koponen *et al*. (1995) considered this species to be aquatic in Finland. Schuster (1974) attributes it to alluvial sand or sandy soil adjacent to streams, in acid late snow areas, on siliceous rock faces receiving water. Like ***Marsupella emarginata*** (Figure 65-Figure 67), it avoids calcareous sites but tolerates frequent inundation. Hong (1980) reported ***Marsupella sparsifolia*** (Figure 80-Figure 81) from soil in the North Cascades Range, Washington, USA. It also occurs on moist cliffs where it can form close mats, as seen along Cliff River in the Huron Mountains, Michigan, USA (Nichols 1935).

Figure 82. ***Marsupella sparsifolia*** habitat. Photo by Kristian Peters (Korseby Online; Sagebud), with permission.

Reproduction

Marsupella sparsifolia (Figure 80-Figure 81) is **paroicous** (Smith 1990). It is usually fertile and frequently produces capsules.

Marsupella sphacelata (Figure 83-Figure 86)

Distribution

Marsupella sphacelata (Figure 83-Figure 86) is Holarctic, occurring in boreal and low-Arctic regions (Schuster 1974). Its terrestrial form extends further south than does the aquatic form. This species is widespread in Europe, from Greenland southward to England, Spain, and the Azores. It is widespread in Japan, but is poorly known elsewhere in Asia. In North America it extends from Alaska south to California and in the east from Newfoundland to North Carolina.

Figure 83. ***Marsupella sphacelata*** clone. Photo by Hermann Schachner, through Creative Commons.

Figure 84. ***Marsupella sphacelata***, a boreal and low-Arctic species mostly of slow streams. Photo by Štěpán Koval, with permission.

Figure 85. ***Marsupella sphacelata***. Photo by Giovanni Bergamo Decarli, through Creative Commons.

Figure 86. ***Marsupella sphacelata*** showing its mat growth habit and dark pigments. Photo by Hermann Schachner, through Creative Commons.

Aquatic and Wet Habitats

Watson (1919) considered ***Marsupella sphacelata*** (Figure 83-Figure 86) to be an alpine species submerged in fast water. Geissler (1975) likewise found it in European alpine streams. At 1400 m in the Sayan Mountains of southern Siberia, Konstantinova and Vasiljev (1994) reported it submerged on rocks in brooks, mixed with other liverworts. But in the eastern USA, it occurs in mountain streams that are not alpine (Glime 1968), and Vieira *et al*. (2005) found it in mountain streams of northwest Portugal. Sharp (1939) reported it from boulders in brooks in Tennessee, USA, where it was rare. It also occurs on a rock cliff associated with Katrine Lake in Sudbury, Ontario, Canada and on wet rock of a small stream at Pinetree Lake in Algonquin Park at 600 m or less, also in Ontario (Williams & Cain 1959). At Cumberland Falls State Park (327 m) in Kentucky, USA, it occurred on moist rocks (Norris 1967).

Koponen *et al*. (1995) considered this species to be aquatic in Finland. The typical aquatic form grows attached to rocks and rock walls of mountain streams, usually in small pools and in slow water (Figure 87) (Schuster 1974). It seems to be absent from calcareous rocks. It can form pure patches, but also grows with ***Marsupella emarginata*** (Figure 65-Figure 67), ***Scapania undulata*** (Figure 60), and ***S. subalpina*** (Figure 88). Its lax tufts are typically dull green and brownish-tinged above (Figure 83-Figure 86, Figure 89).

Figure 87. ***Marsupella sphacelata*** in submersed habitat. Photo by Hermann Schachner, through Creative Commons.

Figure 88. ***Scapania subalpina***, a species that often grows with ***Marsupella sphacelata*** in mountain streams. Photo by Andy Hodgson, with permission.

But ***Marsupella sphacelata*** (Figure 83-Figure 86) can also be found in wet areas not associated with streams. Kitagawa (1978a) found it to be locally abundant on damp soil at the edge of moors below the summit of Odake, Japan.

Adaptations

The terrestrial forms of ***Marsupella sphacelata*** (Figure 83-Figure 86) are able to grow in direct sun, often with intermittent seepage (Figure 89) (Schuster 1974). They are able to endure long dry periods. Their life form is small to large tufts (Smith 1990). These forms create blackish patches. This attests to a wide physiological range for the species (Schuster 1974).

Marsupella sphacelata (Figure 83-Figure 86, Figure 89) can produce UV-B-absorbing compounds (Figure 86, Figure 89) in mountain streams where this radiation is high. Arróniz-Crespo *et al*. (2004) verified that these differed among populations, but we need to verify whether these are environmentally induced or genetically different.

Reproduction

Marsupella sphacelata (Figure 84-Figure 87, Figure 89) is **dioicous** (Smith 1990). Fertile plants are rare and capsules very rare.

Figure 89. ***Marsupella sphacelata*** habitat on wet substrate, showing dark pigments that absorb UV radiation. Photo by Hermann Schachner, through Creative Commons.

Marsupella subemarginata (Figure 90)

Distribution

Collections of ***Marsupella subemarginata*** (Figure 90) thus far suggest that it is **oro-boreal** (boreal mountains and mountainous regions), with records from Switzerland, Russia, and Japan (Bakalin *et al.* 2019b).

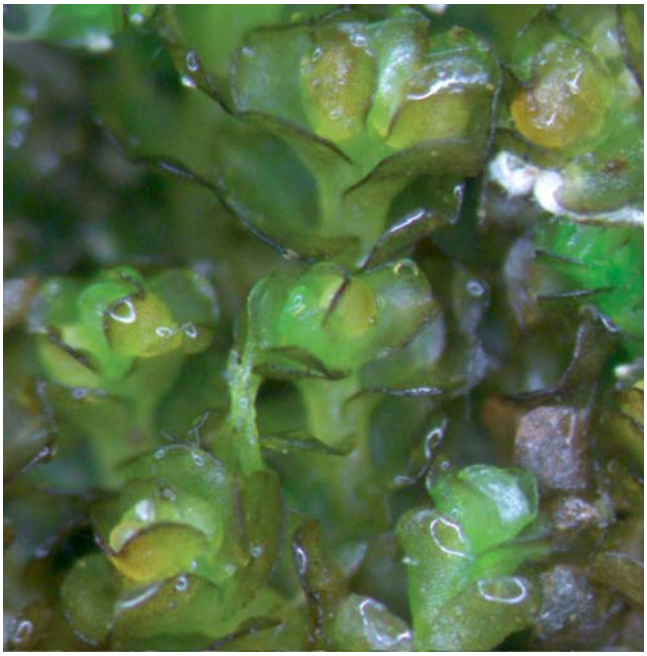

Figure 90. ***Marsupella subemarginata***, a species from an Eastern Hemisphere oro-boreal region. Photo modified from Bakalin *et al.* 2019; permission pending.

Aquatic and Wet Habitats

Marsupella subemarginata (Figure 90) occurs on temporarily wet cliffs and boulders in areas with a mild climate and even distribution of precipitation around the year (Bakalin *et al.* 2019). In Kamchatka it occur on moist boulders near temporary streams in mountain tundra.

Adaptations

Plants of ***Marsupella subemarginata*** (Figure 90) are greenish brownish to rusty (Bakalin *et al.* 2019); the darker colors can filter out the high UV light one would expect in its mountain environments. Its stem has marginal cells of the hyaloderm with thickened walls on all sides (Figure 91), possibly protecting them from gushes of water when it rains or preventing water loss when it does not. Nevertheless it has few rhizoids.

Reproduction

Although ***Marsupella subemarginata*** (Figure 90) is **dioicous**, Bakalin and coworkers (2019) reported it as freely producing spores that frequently germinate within the cushions.

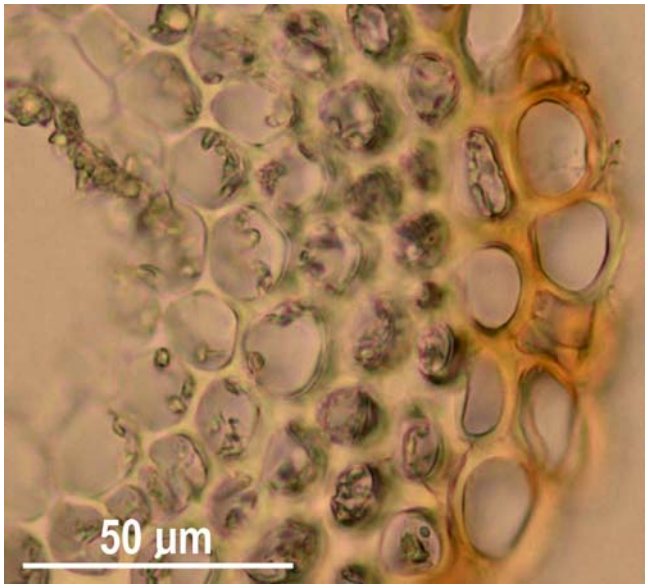

Figure 91. ***Marsupella subemarginata*** stem cross section showing thickened walls on the epidermal cells. Photo modified from Bakalin *et al*. 2019; permission pending.

Biochemistry

There seem to no studies on the biochemistry of ***Marsupella subemarginata*** (Figure 90) and oil bodies are not described (Figure 92).

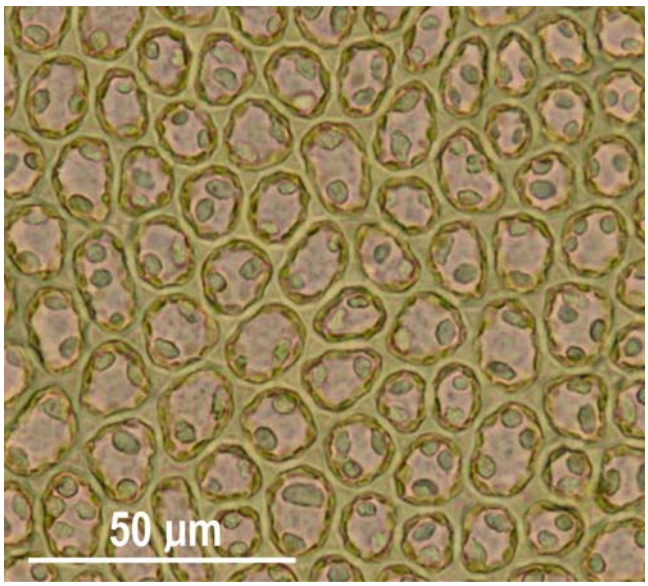

Figure 92. ***Marsupella subemarginata*** leaf cells with oil bodies? Photo modified from Bakalin *et al.* 2019; permission pending.

Marsupella vietnamica (Figure 93)

Distribution

So far, ***Marsupella vietnamica*** (Figure 93) is known only from North Vietnam, but Bakalin and coworkers suggest it should be found in Yunnan, China, as well (Bakalin *et al.* 2019b).

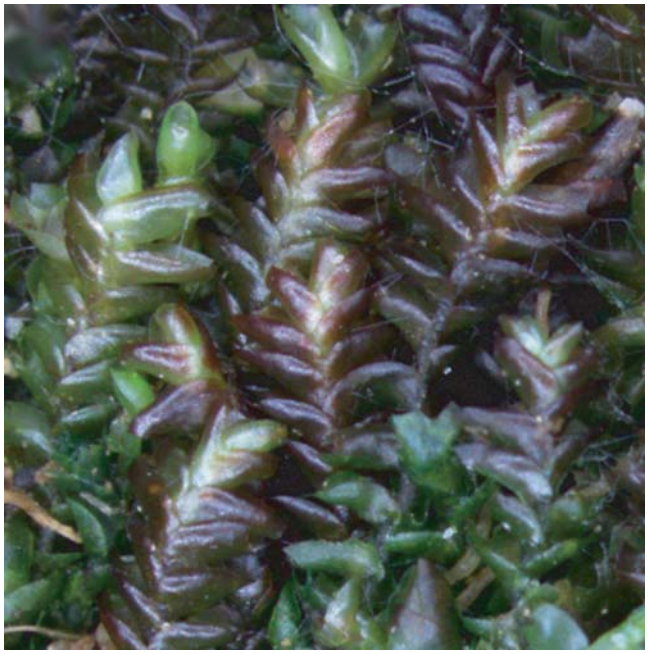

Figure 93. ***Marsupella vietnamica***, a species from North Vietnam. Photo modified from Bakalin *et al.* 2019; permission pending.

Aquatic and Wet Habitats

Marsupella vietnamica (Figure 93) is thus far a meso-hygrophytic species and an acidophile. It prefers shaded to semi-open moist to wet cliffs near streams where there is sufficient water even during the so-called "dry season" in the tropical zone. The species occurs in middle mountain elevations.

Adaptations

No special adaptations seem to be described for ***Marsupella vietnamica*** (Figure 93). The stem appears to have somewhat thickened walls in the outer layers (Figure 94). The leaf cells have huge trigones and in the photo they have brown cell walls (Figure 95).

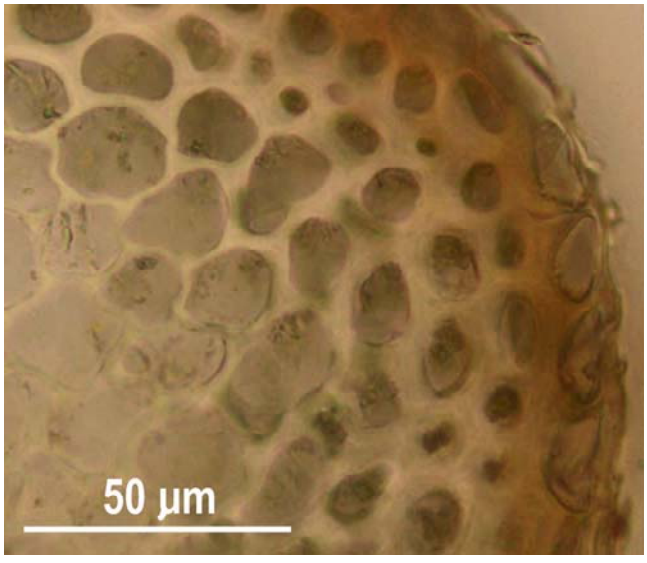

Figure 94. ***Marsupella vietnamica*** stem cross section. Photo modified from Bakalin *et al.* 2019; permission pending.

Reproduction

The sexual condition is unknown, but Bakalin *et al.* (2019b) indicated that ***Marsupella vietnamica*** (Figure 93) is **probably dioicous** because they found no antheridia or sporophytes.

Biochemistry

There seem to be no studies on the biochemistry of ***Marsupella vietnamica*** (Figure 93), but there appear to be distinct oil bodies in the leaf cells (Figure 95).

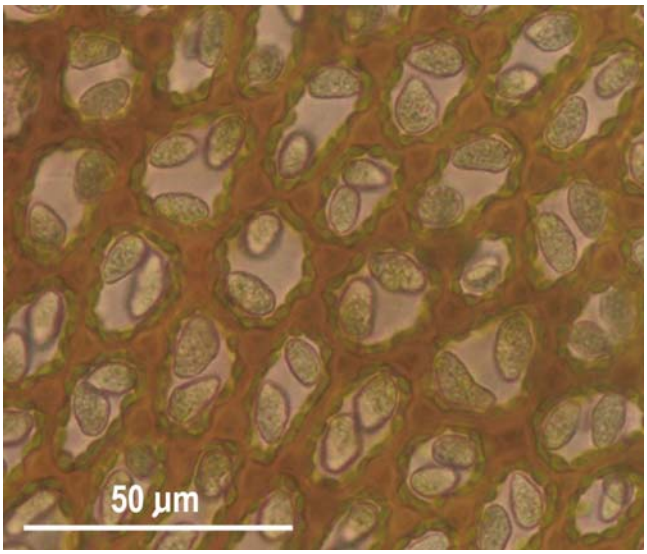

Figure 95. ***Marsupella vietnamica*** leaf cells and oil bodies? Photo modified from Bakalin *et al.* 2019; permission pending.

Marsupella yakushimensis

Distribution

Marsupella yakushimensis is a south temperate to subtropical Montane East Asian endemic species known in China, the southern part of the Korean peninsula, and the southern half of Japan (Bakalin *et al*. 2021).

Aquatic and Wet Habitats

Marsupella yakushimensis is an acidophilic hygro- to hydrophyte (Bakalin *et al*. 2021). It occurs on wet cliffs at some distance from water courses or on stones washed with sluggishly running water in partly shaded habitats in the middle elevations of mountains with evergreen to deciduous broadleaved forests. Choi *et al*. (2012, 2013) found it on humid soil of a steep mountain slope and on wet cliffs along a stream in Korea.

Adaptations

Commonly, ***Marsupella yakushimensis*** forms pure patches, but more rarely it is associated with ***Scapania undulata*** (Bakalin *et al*. 2021). It can have purple to red pigmentation, especially in Japanese populations, perhaps protecting it from UV light in the mountains.

Reproduction

Marsupella yakushimensis is **dioicous** and seems to produce antheridia regularly, but it rarely has archegonia (Bakalin *et al*. 2021). Even where Bakalin *et al*. found the two sexes intermixed there was no evidence of fertilization or a fully developed perianth.

Nardia assamica

Distribution

Nardia assamica is an east Asian species that extends into the Caucasus (Bakalin *et al*. 2009), but also extends into alpine areas in Europe (Geissler 1975) and Australia (ITIS 2020c). Hicks (2003) also includes Alaska.

Aquatic and Wet Habitats

Geissler (1975) reported ***Nardia assamica*** in European alpine streams. Hicks (2003) listed its habitats as wet exposed soil with water seepage. Bakalin *et al*. (2009) reported on its presence in the South Kuril Islands, East Asia. There, its less aquatic habitats, compared to those in the alpine streams, include oligotrophic peatlands, wet open places, fumaroles and hot sulfur springs at 50ºC, areas of bare clayish or sandy ground in places with destroyed vegetation cover (stream banks, travertine cones in hot stream areas), rocks along cool and hot sulfur springs in forested and forestless areas, cliff wall in *Salix-Duscheckia* wet community, among mosses in hummocks in sedge-moss mires, between patches of ***Eriophorum*** (Figure 96) and ***Eleocharis*** (Figure 22) in wet depression in wind-stressed community of ***Sasa*** (bamboo; Figure 97) and small herbs. It frequently occurs with other leafy liverworts.

Figure 96. ***Eriophorum scheuchzeri*** in the Swiss Alps. ***Nardia assamica*** lives among plants of this genus in the Alps. Photo by Simon A. Eugster, through Creative Commons.

Figure 97. ***Sasa*** ground cover in spruce forest at Bihora Pass Japan. ***Nardia assamica*** lives in association with ***Sasa*** in wet depressions. Photo by Janice Glime.

Biochemistry

The oil bodies are large (Figure 98). Although there seem to be no biochemical studies, one could conjecture that such large oil bodies might contain some interesting biochemicals.

Figure 98. ***Nardia assamica*** cells showing large oil bodies. Photo by Yang Jia-dong, Taiwan Encyclopedia of Life, through Creative Commons.

Nardia compressa (Figure 99-Figure 102)

(syn. = *Alicularia compressa*)

Distribution

Nardia compressa (Figure 99-Figure 102) has a worldwide distribution, but avoids the hot tropics, occurring there only at high elevations (DiscoverLife.org 2020).

Figure 99. ***Nardia compressa***, a species with worldwide distribution outside the tropics, occurring in lakes and streams. Photo by Hermann Schachner, through Creative Commons.

Figure 100. ***Nardia compressa*** showing stoloniferous shoots. Photo by Hermann Schachner, through Creative Commons.

Aquatic and Wet Habitats

Based on early studies, West (1910) reported ***Nardia compressa*** (Figure 99-Figure 102) to be abundant on wet and submersed rocks (Figure 101) in Scotland, sometimes occurring down to 1 m depth in lakes. Light (1975) reported it from small lakes of the Scottish mountains where it experiences 4-7 months of ice cover and low ion concentrations.

Figure 101. ***Nardia compressa*** habitat by a stream. Photo by Hugues Tinguy, with permission.

Watson (1919), on the other hand, reported ***Nardia compressa*** (Figure 99-Figure 102) as a species submerged in slow water with poor mineral salts, as well as rocky and stony beds of fast streams. In the Haute Ardenne rivers of Belgium it seems to be strictly aquatic (Leclercq 1977). In Thuringia, Germany, Marstaller (1987) found it in association with ***Platyhypnidium*** (Figure 68) and ***Fontinalis antipyretica*** (Figure 69).

Lepp (2012) reported ***Nardia compressa*** (Figure 99-Figure 102) from the edges of a small stream running through a steep ravine in Alaska. In swift mountain streams of Yakobi Island, Alaska, USA, Shacklette (1965) found that the intertwined stems can dam the stream, creating a series of terraced pools. The growth of the liverwort closes the pool surface (*e.g.* Figure 102), permitting tracheophytes to invade the mat.

Vieira *et al*. (2004, 2005) described ***Nardia compressa*** (Figure 99-Figure 102) in Portugal as the dominant species from granite slabs of the streambed, where it is immersed, often in fast-flowing acidic water. It is most common in high mountain areas, but often in exposed peat bog areas at 700-1400 m asl. It seems to form extensive populations anywhere it can become established. This includes exposed peat bog areas associated with ***Fissidens polyphyllus*** (Figure 103), ***Marsupella aquatica*** (Figure 59-Figure 62), ***Marsupella sphacelata*** (Figure 83-Figure 87), ***Platyhypnidium lusitanicum*** (Figure 104), and ***Scapania undulata*** (Figure 60), in these mountain streams of northwest Portugal (Vieira *et al*. 2005).

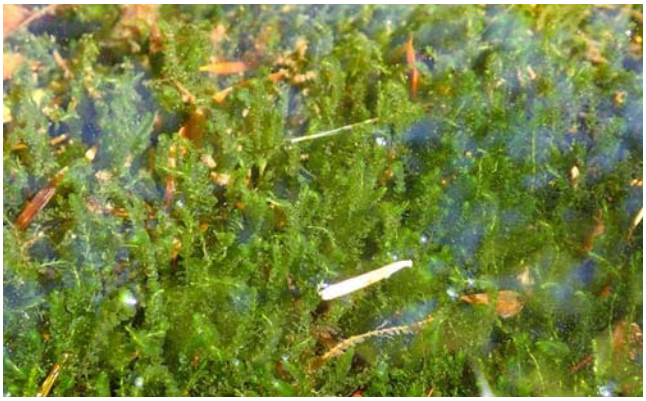

Figure 102. ***Nardia compressa*** submersed. Photo by Hugues Tinguy, with permission.

Figure 103. ***Fissidens polyphyllus***, a species that occurs with ***Nardia compressa*** in exposed peat bog areas. Photo by David T. Holyoak, with permission.

Figure 104. ***Platyhypnidium lusitanicum***, an associate with ***Nardia compressa***. Photo by Barry Stewart, with permission.

Geissler (1975) considered ***Nardia compressa*** (Figure 99-Figure 102) to be a helokrene species associated with alpine streams. Ferreira *et al*. 2008) considered it to be a species of rivers. Scarlett and O'Hare (2006) found it to be among the commonest species in English and Welsh rivers.

Nardia compressa (Figure 99-Figure 102) apparently is unable to tolerate alkaline water well. Wilkinson and Ormerod (1994) studied the effects of catchment liming on bryophytes in upland Welsh streams. ***Nardia compressa*** had the greatest cover exhibited in any one stream, reaching up to 71% cover. Liming was used to restore acidified streams. Under this treatment, the cover of ***N. compressa*** declined significantly from 39% to 5%.

Rothero (2020) found it on permanently wet or frequently inundated rocks and stones in acidic turbulent streams and rivers. It can occasionally be embedded in sand and gravel. It typically forms spongy masses, especially in cold, slow-flowing headwaters of upland streams, but it also occurs in **burns** (streams or small rivers) and flushes associated with late-lying snow fields, often forming pure patches of many square meters.

Adaptations

Nardia compressa (Figure 99-Figure 102) varies in color from deep green to reddish-brown or deep purple (Smith 1990). The plants are robust and form large tufts.

Reproduction

Nardia compressa (Figure 99-Figure 102) is **dioicous** and is rarely fertile in the UK (Smith 1990). Gemmae are unknown.

Nardia geoscyphus (Figure 105-Figure 106)

Distribution

Nardia geoscyphus (Figure 105-Figure 106) is a boreal species occurring in Europe, Asia, and North America (Natcheva 2020). Overall, it has a restricted distribution with low population density (Natcheva 2020).

Figure 105. ***Nardia geoscyphus***, a boreal Northern Hemisphere species from stream banks and constructed ditches. Photo by Štěpán Koval, with permission.

Figure 106. ***Nardia geoscyphus*** habitat on a stream bank. Photo by Martine Lapointe, with permission.

Beaucourt *et al*. (1987) reported ***Nardia geoscyphus*** (Figure 105) from irrigation ditches. It also grows on eroded soil beside roads and on stream banks (Figure 106) (Natcheva 2020).

Adaptations

Nardia geoscyphus (Figure 105-Figure 106) rarely occurs in dense **mats** and the shoots are usually prostrate and closely adhere to the soil (Evans 1912). Rhizoids are numerous (Smith 1990). Its coloration ranges from green to reddish brown or purplish . It often grows among other bryophytes, likely retaining more water due to their presence.

Reproduction

Nardia geoscyphus (Figure 105-Figure 106) is **paroicous** (having archegonia and antheridia on same branch), permitting it to frequently produce capsules (Smith 1990).

Nardia scalaris (Figure 107-Figure 108, Figure 111)

(syn. = *Alicularia scalaris*, *Alicularia scalaris* var. *distans*, *Alicularia scalaris* var. *procerior*, *Alicularia scalaris* var. *rivularis*)

Distribution

Nardia scalaris (Figure 107-Figure 108, Figure 111) is distributed in the North Pacific in Alaska, British Columbia, California, Oregon, Washington in North

America; Chukotka, Kamchatka, Magadan, and Sakhalin in Russia (Bakalin 2012). Elsewhere, it is reported from Tennessee, USA (Sharp 1939), Scotland (West 1910), Serbia (Pantović & Sabovljević 2013), and the Azores (Sjögren 1997). ITIS (2020d) also reports it from southern Asia and Africa.

Figure 107. ***Nardia scalaris***, a species from the Northern Hemisphere, southward into the mountains, growing on peaty soils and in springs. Photo by J. C. Schou, with permission.

Figure 108. ***Nardia scalaris*** forming continuous carpet. Photo by Hermann Schachner, through Creative Commons.

Figure 109. ***Saxifraga ferruginea***, a species that can grow on carpets of ***Nardia scalaris*** in Alaska. Photo by Paul Slichter, with permission.

Aquatic and Wet Habitats

West (1910) reported ***Nardia scalaris*** (Figure 107-Figure 108, Figure 111) from wet sandy-peaty shores in Scotland, where it is often abundant. Also in Scotland, Harriman and Morrison (1982) found ***Nardia scalaris*** [and several ***Scapania*** (*e.g.* Figure 60) species] to be the most abundant species of bryophytes in the streams. Watson (1919) described it as a species submerged in fast water, on ground or rocks, on banks with frequent submergence and slow water, and in usually drier sites with fast water.

Sharp (1939) reported it on moist, peaty soil in Tennessee, USA, but there it was rare, being more common farther north. Pantović and Sabovljević (2013) found ***Nardia scalaris*** (Figure 107-Figure 108, Figure 111) on rock by a stream and on soil on Mt. Boranja in western Serbia. Sjögren (1997) found it in a single collection as "accidentally" epiphyllous in the Azores Islands.

In Alaska ***Nardia scalaris*** (Figure 107-Figure 108) can form continuous carpets (Figure 108) that seem to support the growth of ***Saxifraga ferruginea*** (Figure 109) (Shacklette 1961). These areas typically are highly disturbed and contaminated with copper, for which these two species seem to have good tolerance. The liverwort provides an organic layer about 1 cm thick. It grows on a variety of substrates and is tolerant of the sulfide found in pyrite. It is often a snowbed species and has a strong requirement for abundant water and light with little or no competition.

The ***Scapania*** (Figure 60)-***Nardia*** (Figure 107-Figure 108, Figure 111) community on Yakobi Island colonizes mountain rivulets, forming carpets that permit ***Nephrophyllidium crista-galli*** (syn. = *Fauria crista-galli*; Figure 110) to colonize and eventually succeed to a copperbush community (Shacklette 1965).

It is likely that this species has some salt tolerance, as Evans (1912) reported it growing on cliffs at about 3 m above the high tide level in Nova Scotia and New Brunswick, Canada.

Reproduction

Nardia scalaris (Figure 107-Figure 108, Figure 111) is **dioicous** and rarely produces capsules (Figure 111), at least in North America (Evans 1912; Smith 1990). It typically produces prostrate shoots that become suberect when growing in compact mats.

Figure 110. ***Nephrophyllidium crista-galli***, a species that colonizes the ***Scapania-Nardia*** community on Yakobi Island. Photo by Andy Tasler, through public domain.

Figure 111. ***Nardia scalaris*** with capsules. Photo by J. C. Schou, with permission.

Fungal Interactions

Bidartondo and Duckett (2010) found that ***Nardia scalaris*** (Figure 107-Figure 108, Figure 111) predominantly and consistently associates with the ***Sebacina vermifer*** species complex (see Figure 169). An unusual find was that the DNA sequence of the fungus on this liverwort was identical to that on ***Lophozia ventricosa*** (Figure 112) at Ben Wyvis, Scotland. The only other shared DNA found in their study was for this fungus species on both ***Nardia scalaris*** and ***Schistochilopsis opacifolia*** at St. Gotthard, Switzerland. But what are the biological implications of this shared DNA, other than a local population that is able to inhabit more than one host? Does it mean it did so recently?

Biochemistry

This species has been the subject of a number of biochemical studies. Beneš *et al*. (1981) reported on a triterpenoid present in the species, one already known from other liverworts. Then they found a new diterpenoid, nardiin, from the species (Beneš *et al*. 1982). Langenbahn *et al*. (1993) further described terpenes from the species, revealing 12 diterpene malonates. The aromatic compounds give ***Nardia scalaris*** (Figure 107-Figure 108, Figure 111) its distinctive carrot-like odor (Beike *et al*. 2010).

Figure 112. ***Lophozia ventricosa***, a liverwort that shares the fungus ***Sebacina vermifer*** with the same DNA as that of the one on ***Nardia scalaris***. Photo by Hermann Schachner, through Creative Commons.

Harpanthaceae

Harpanthus flotovianus (Figure 113-Figure 116)

Distribution

Harpanthus flotovianus (Figure 113-Figure 116) occurs in Europe, Asia, and North America (ITIS 2020e), where it is widespread in boreal and montane regions.

Aquatic and Wet Habitats

In early records, ***Harpanthus flotovianus*** (Figure 113-Figure 116) was found on the sides of fast alpine streams (Watson 1919). Koponen *et al*. (1995) considered it to be aquatic in Finland. In eastern Fennoscandia it occurs in wet habitats – near springs and streams, and in fens and moist forests (Figure 117) (Järvinen 1976). Dulin (2015) reported it from the vicinities of glacial relict lakes, occurring on decaying wood in herbal-***Sphagnum*** mixed and birch forests. It occurred there in pure patches and with other liverworts.

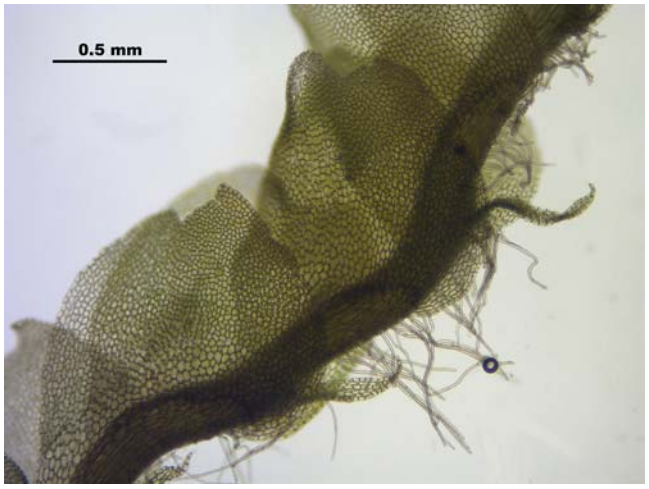

Figure 113. ***Harpanthus flotovianus***, a widespread boreal-montane species, occurring in streams, springs, lakes, their banks, and other wet habitats. Photo by Hermann Schachner, through Creative Commons.

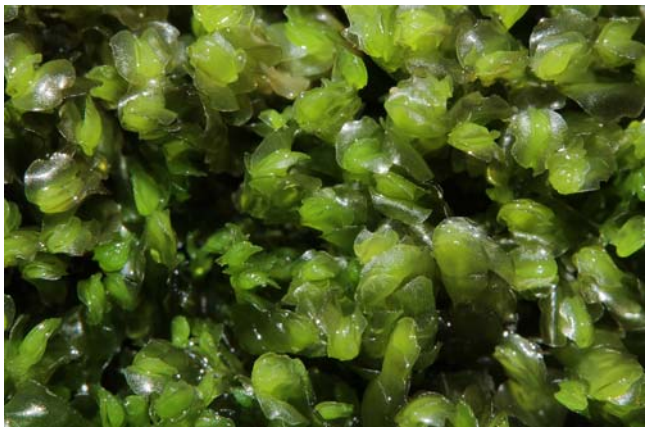

Figure 114. ***Harpanthus flotovianus***. Photo by Hermann Schachner, through Creative Commons.

Figure 115. ***Harpanthus flotovianus***. Photo by Štěpán Koval, with permission.

Figure 116. ***Harpanthus flotovianus*** showing its mat growth. Photo by Hermann Schachner, through Creative Commons.

Figure 117. ***Harpanthus flotovianus*** habitat in a wet spruce opening. Photo by Scot Loring, through Creative Commons.

In Estonia, ***Harpanthus flotovianus*** (Figure 113-Figure 116) occurs in fens, transitional mires, and bogs (Figure 118) (Ingerpuu *et al*. 2014). Emerson and Loring (2010) likewise found it associated with ***Sphagnum*** in the Rogue River-Siskiyou National Forest. In this forest it formed an association including ***Calypogeia sphagnicola*** (Figure 44-Figure 46), ***Pohlia sphagnicola*** (Figure 119), ***Cephaloziella spinigera*** (Figure 120), and ***Kurzia makinoana*** (Figure 121.

Figure 118. Peatland habitat suitable for ***Harpanthus flotovianus*** and associated ***Pohlia sphagnicola***. Photo by Michael Lüth, with permission.

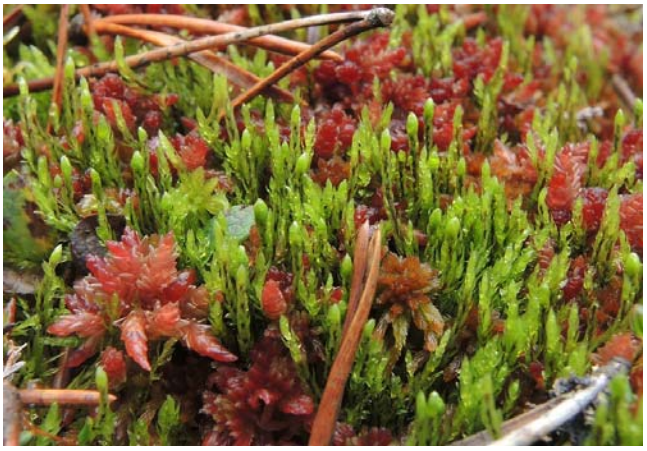

Figure 119. ***Pohlia sphagnicola***, often an associate of ***Harpanthus flotovianus*** in bogs and poor fens. Photo by Michael Lüth, with permission.

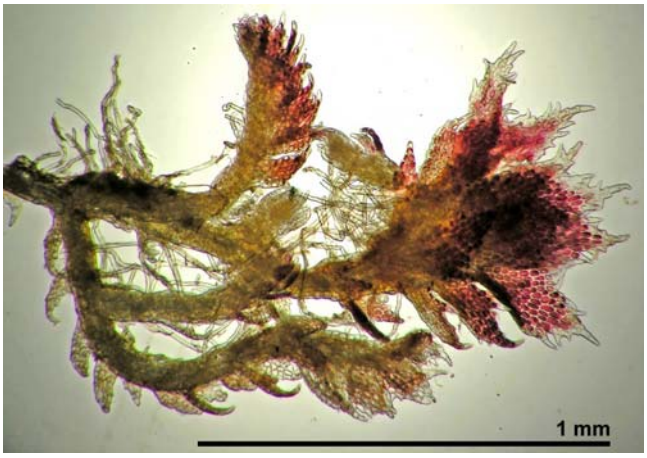

Figure 120. ***Cephaloziella spinigera*** autoicous shoot, an associate of ***Harpanthus flotovianus*** in bogs and poor fens. Photo by David Wagner, with permission.

Figure 121. ***Kurzia makinoana***, an associate of ***Harpanthus flotovianus*** in bogs and poor fens. Photo by Blanka Aguero, with permission.

Reproduction

Fertile plants of ***Harpanthus flotovianus*** (Figure 113-Figure 116) are unknown in the Pacific Northwest (Schofield 2002) and are rare in the British Isles (Paton 1999), where they are **dioicous** (Smith 1990). The paucity of sexual reproduction and lack of gemmae undoubtedly contributes to the rarity in this region. The species is perennial and should be identifiable throughout the year.

Fungal Interactions

Wang and Qiu (2006) found no records of any associated mycorrhizal fungus with this species.

Hygrobiellaceae

Hygrobiella laxifolia (Figure 122)

Distribution

Hygrobiella laxifolia (Figure 122) occurs in Europe, Asia, and North America. However, in 2014, Bakalin and Vilnet explored the genomic makeup of populations from northwestern Europe, Far Eastern Russia, and western USA. They found that the Far Eastern specimens separated from each other and from the North American population. They named the Far Eastern clades as ***Hygrobiella intermedia*** and ***Hygrobiella squamosa***. These two species and ***Hygrobiella laxifolia*** are **sympatric** (sharing part of their distributional area) in the northern Pacific region. Pigmentation, form of perianth and leaves, stem cross section anatomy, and length of underleaves can be used to separate the species morphologically.

Aquatic and Wet Habitats

Under the name of ***Hygrobiella laxifolia*** (Figure 122), Nichols (1918) reported the species from a rock ravine streambank on Cape Breton Island, Canada. Watson (1919) considered it to be subalpine, occasionally being submerged. Koponen *et al*. (1995) considered populations under this name to be aquatic in Finland.

Luis *et al*. (2007) reported populations from Madeira Island off the northwest coast of Africa as ***Hygrobiella laxifolia*** (Figure 122). It grew on rocks in the spray zone

of the stream margins where it was associated with other bryophytes.

Figure 122. ***Hygrobiella laxifolia***, a Northern Hemisphere species of stream banks. Photo by Martine Lapointe, with permission.

Adaptations

The plants of ***Hygrobiella laifolia*** range in color from green to greenish-brown or reddish-brown (Smith 1990). Its ability to grow mixed with other bryophytes can help it to maintain hydration.

Reproduction

Hygrobiella laxifolia is **dioicous** (Smith 1990).

Jungermanniaceae

Eremonotus myriocarpus (Figure 123-Figure 126)

Distribution

Eremonotus myriocarpus (Figure 123-Figure 126) is distributed in Europe, Asia, and North America (ITIS 2020f). The species is a rather rare Arctic-alpine species from north and central Europe, China, Japan, the Far East of Russia, and several localities in Greenland and North America (Konstantinova & Savchenko 2008). Although records are widespread, they are not frequent.

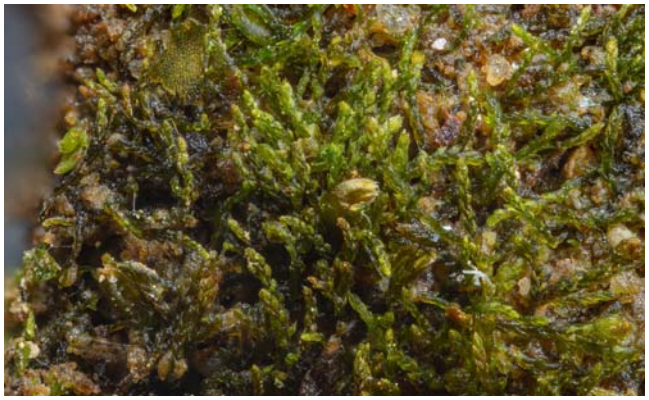

Figure 123. ***Eremonotus myriocarpus***, a rather rare Arctic-alpine species in the Northern Hemisphere, where it is occasionally submerged. Photo by Kristian Peters, with permission.

Figure 124. ***Eremonotus myriocarpus*** showing a green mat form. Photo by Kristian Peters, with permission.

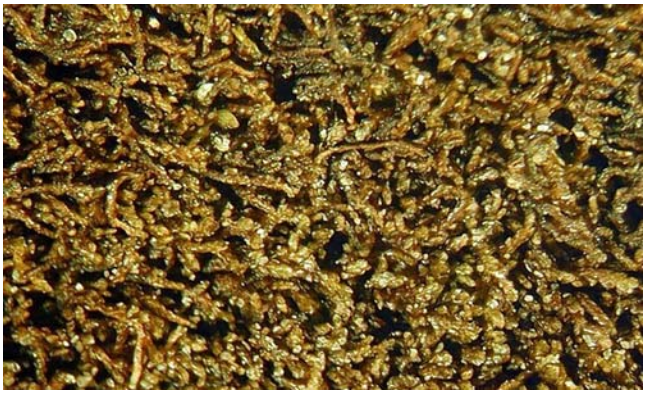

Figure 125. ***Eremonotus myriocarpus*** showing a color variant, perhaps in response to high light intensity. Photo by Michael Lüth, with permission.

Aquatic and Wet Habitats

Watson (1919) considered this to be a subalpine species that is occasionally submerged (Figure 126). Long (1982) reported it from a damp rock face.

Figure 126. ***Eremonotus myriocarpus*** habitat. Photo by Michael Lüth, with permission.

Adaptations

Eremonotus myriocarpus is minute (Smith 1990). It forms reddish-brown patches, a color uncommon in most submersed species, but beneficial for species in exposed sites. The coloration, however, is also advantageous in cold habitats, even when the plants are submersed.

Reproduction

Eremonotus myriocarpus is **dioicous** (Smith 1990). It lacks gemmae. In the United Kingdom, male plants are frequent while female plants are only occasional.

Fungal Interactions

Fungi seem to find this species to be a suitable habitat. However, Bidartondo and Duckett (2010) found only Ascomycetes in the usually basidiomycete-containing ***Eremonotus myriocarpus*** (Figure 123-Figure 126) from locations in Europe.

Jungermannia (Figure 127-Figure 128, Figure 130-Figure 133, Figure 135-Figure 137, Figure 140-Figure 143)

Jungermannia (Figure 127-Figure 128, Figure 130-Figure 133, Figure 135-Figure 137, Figure 140-Figure 143) ***vs. Solenostoma*** (Figure 170-Figure 176, Figure 177-Figure 189, Figure 193-Figure 196) – These two genera have been divided and many species have been moved to ***Solenostoma***. They occur in small lakes in southern Finland (Toivonen & Huttunen 1995), small, pristine streams of the Tolvajärvi region, Russian Karelia (Vuori *et al*. 1999), and occur as west African rheophytes (Shevock *et al*. 2017).

Jungermannia atrovirens (Figure 127-Figure 128, Figure 130)

(syn. = *Aplozia riparia*, *Aneura riparia* fo. *potamophila*, *Aneura riparia* var. *rivularis*, *Aplozia riparia* var. *rivularis*, *Haplozia riparia* var. *potamophila*, *Haplozia riparia* var. *rivularis*, *Jungermannia riparia*, *Plectocolea riparia*, *Solenostoma triste*)

Distribution

Jungermannia atrovirens (Figure 127-Figure 128, Figure 130) is listed by ITIS (2020g) for Europe, Asia, Africa, and North America.

Aquatic and Wet Habitats

Jungermannia atrovirens (Figure 127-Figure 128, Figure 130) is often completely submerged and truly aquatic in fast streams, on banks with frequent submergence and slow water, and wet, rocky places associated with fast water (Watson 1919). This description is supported by its occurrence in the Linth River, Switzerland (Koch 1936); in water in Westfalens, northwestern Germany (Koppe 1945); the only bryophyte in four streams of the Black Mountain District of South Wales (Jones 1948); hydrophytic or hydrophilic in the Rhine area, Germany (Philippi 1968); among the most common in upstream and extreme upper reaches and tributaries of the River Tweed, UK (Holmes & Whitton 1975b; Birch *et al*. 1988); above (Figure 128) and below water in the upper reaches of the River Wear, UK (Holmes & Whitton 1977a); in the river and on the river bank of the River Tees, UK (Holmes & Whitton 1977b); in upper to midstream of the River Swale, Yorkshire, UK (Holmes & Whitton 1977c); throughout the River Tyne, UK (Holmes & Whitton 1981); in the ***Platyhypnidium*** (Figure 68)-***Fontinalis antipyretica*** (Figure 69) association, Thuringia, Germany (Marstaller 1987); among the commonest species in English and Welsh rivers (Scarlett & O'Hare 2006); at spring and river in Tara River canyon and Durmitor area, Montenegro (Papp & Erzberger 2011); and on damp rock face in the Canary Islands (Crundwell *et al*. 1978).

Figure 127. ***Jungermannia atrovirens***, a relatively widespread, predominantly Northern Hemisphere species submerged in streams and lakes. Photo by Hermann Schachner, through Creative Commons.

Figure 128. ***Jungermannia atrovirens*** wet above the water level. Photo by Bernd Haynold, through Creative Commons.

In the UK this species grows in a variety of calcareous situations, including rock, tufa, or soil. On sandstone cliffs, as well as limestone cliffs, it is abundant. But it also occurs on less wet habitats, including forestry tracks with limestone or tufaceous rock. Konstantinova *et al*. (2009) reported it from moist cliffs and rocks on stream banks, primarily in calcium-rich sites. Birk and Willby (2010) considered it to be a species of siliceous mountain brooks, indicating a high quality site, but less frequently than ***Scapania undulata*** (Figure 60) or ***Chiloscyphus polyanthus*** (Figure 129).

Figure 129. ***Chiloscyphus polyanthos***, a frequent species in siliceous mountain brooks where ***Jungermannia atrovirens*** is able to grow. Photo by Hermann Schachner, through Creative Commons.

Adaptations

Jungermannia atrovirens is small, forming yellowish-green to dull green patches (Smith 1990). It often grows through patches of other bryophytes where they can help it to retain moisture.

Reproduction

Although the species is **dioicous**, males and females (Figure 130) are typically both abundant (BBS 2020), reducing the disadvantage of separate sexes. Although perianths are frequent, capsules are produced only occasionally in the UK, in spring and summer (Smith 1990).

Figure 130. ***Jungermannia atrovirens*** with abundant perigynia. Photo by Hugues Tinguy, with permission.

Jungermannia borealis (Figure 131)

Distribution

The distribution of ***Jungermannia borealis*** (Figure 131) must be viewed with caution because of a number of misidentifications. It seems to be in northern Europe, Asia, and North America, extending southward in the mountains.

Figure 131. ***Jungermannia borealis*** with perigynium, a species of the Northern Hemisphere, living on stream and river banks and near waterfalls. Photo by Des Callaghan, with permission.

Aquatic and Wet Habitats

Jungermannia borealis (Figure 131) occurs in water near a waterfall of the Upper Bureya River (Russian Far East) (Konstantinova *et al*. 2002). In Yakutia, also in Asian Russia, this species occurs on stream and river banks in the upper course of the Indigirka River (Sofronova 2018). Damsholt and Váňa (1977) describe the habitat as typically in basic on shaded rocks and soil.

Reproduction

Like most leafy liverworts, this species is **dioicous** (Figure 131) (Damsholt & Váňa 1977).

Fungal Interactions

Wang and Qiu (2006) found no records of fungi associated with this species.

Jungermannia callithrix (Figure 132)

(syn. = *Solenostoma callithrix*)

Distribution

Jungermannia callithrix (Figure 132) is primarily Neotropical (Schumaker & Váňa 1999), but is known off the coast of Africa (Luis *et al*. 2015).

Figure 132. ***Jungermannia callithrix***, a mostly Neotropical species from narrow mountain streams. Photo by Tomas Hallingbäck, with permission.

Aquatic and Wet Habitats

Luis *et al*. (2015) reported it from a low altitude, narrow stream and low flow in mountain streams on Madeira Island off the northwest coast of Africa.

Jungermannia exsertifolia (Figure 133)

Distribution

Jungermannia exsertifolia (Figure 133) is another Northern Hemisphere species, known from Europe, Asia, and North America (ITIS 2020h). There are a few additional outlying locations on islands. It is a widely distributed Holarctic species with considerable morphological variation throughout its range (Zubel 2008). Váňa (1973) considered European populations of this species to differ somewhat from Asian plants and to represent a different subspecies, ***Jungermannia exsertifolia*** subsp. ***cordifolia*** (Figure 135-Figure 140), discussed below. This subspecies occurs in the European sub-arctic-boreal-subalpine region. Records of this species should be viewed with caution because it has been confused with ***Jungermannia atrovirens*** (Figure 127-Figure 128, Figure 130) as well as failure to recognize it as a subspecies in some European records (Zubel 2008).

Figure 133. ***Jungermannia exsertifolia*** is a widely distributed Holarctic species, primarily in cold-water streams. Photo by Paul Bowyer, through Creative Commons.

Aquatic and Wet Habitats

Koponen *et al*. (1995) considered ***Jungermannia exsertifolia*** (Figure 133) to be aquatic in Finland. It occurs in regulated portions of the River Rhine (Vanderpoorten & Klein 1999b) and in the Alpine Rhine to the Middle Rhine (Vanderpoorten & Klein 1999c). Yet few aquatic studies seem to have recorded it.

This species seems to have an aversion to warm water. In sub-Arctic streams of Iceland ranging 7.1 to 21.6°C, it occurs in low densities in cold streams, but it is absent in the warmest streams (Gudmundsdottir *et al*. 2011a, b).

Adaptations

Like most of the species in this family, ***Jungermannia exsertifolia*** ranges in color from dull green to blackish-purple or even black. The dark coloration most likely protects it from photoinhibition in cold streams. It forms tufts or patches. It has few rhizoids, a character that would seem to be a disadvantage in moving water of streams.

Reproduction

Jungermannia exsertifolia is **dioicous** and lacks gemmae (Smith 1990), suggesting that fragmentation may be an important means of reproduction.

Interactions

Jensen *et al*. (2008) found that ***Jungermannia exsertifolia*** (Figure 133) was among the first liverworts that showed good dose-dependent activity against the malaria parasite ***Plasmodium falciparum*** (Figure 134). It is interesting that these liverworts were collected from Iceland where malaria is unknown.

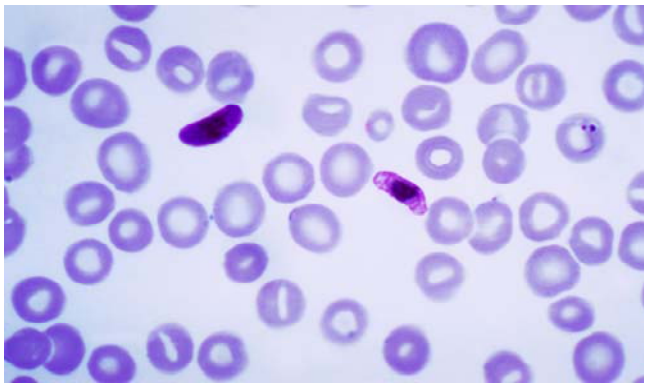

Figure 134. ***Plasmodium falciparum*** macro and microgametocyte. Photo from CDC - Dr. Mae Melvin Transwiki, through public domain.

Jungermannia exsertifolia subsp. *cordifolia* (Figure 135-Figure 137, Figure 140)

(syn. = *Aplozia cordifolia*; *Jungermannia cordifolia*; *Jungermannia eucordifolia*; *Solenostoma cordifolia*)

Distribution

Jungermannia exsertifolia* subsp. *cordifolia (Figure 135-Figure 137, Figure 140) occurs in Europe, Asia, and North America (ITIS 2020i) where it is sub-Arctic-boreal-subalpine in its distribution (Zubel 2008).

Figure 135. ***Jungermannia exsertifolia*** subsp. ***cordifolia***, a sub-Arctic-boreal-subalpine species of fast water. Photo by Des Callaghan, with permission.

Figure 136. ***Jungermannia exsertifolia*** subsp. ***cordifolia*** from a wet habitat. Photo by Des Callaghan, with permission.

Aquatic and Wet Habitats

Nichols (1918) reported this subspecies from ravines on Cape Breton Island, Canada. Watson (1919) considered it to be alpine or subalpine, occurring on submerged rocks in fast water (Figure 137). Geissler (1976) found it in alpine streams in the Swiss Alps. Koponen *et al*. (1995) considered it to be aquatic in Finland; Heino and Virtanen (2006) reported it from streams in northeastern Finland. In Thuringia, Germany, Marstaller (1987) found it in the ***Platyhypnidium*** (Figure 68)-***Fontinalis antipyretica*** (Figure 69) association – a stream association.

Figure 137. ***Jungermannia exsertifolia*** subsp. ***cordifolia*** on a partly submerged rock in fast water. Photo by Dick Haaksma, with permission.

When Martinez-Abaigar *et al*. (1993) transplanted several species of bryophytes to polluted water in the River Iregua in northern Spain, ***Jungermannia exsertifolia*** **subsp.** ***cordifolia*** (Figure 135-Figure 137, Figure 140) proved to be very sensitive to pollution events; ***Fontinalis antipyretica*** (Figure 69) was more tolerant. This research team (Martínez-Abaigar *et al*. 2002) also found that this subspecies accumulated phosphorus (P) and potassium (K) dependent on the concentration of KH_2PO_4 in the water in 15 days of exposure. However, K accumulations fluctuated rather widely, presumably due to the ease with which it can be leaked from the cells. The accumulation of P in the liverwort seems to reach saturation at 20 mg L^{-1}. Increasing the P concentration in the water and tissues failed to increase net photosynthesis. The researchers suggested that the liverwort might be deficient in other mineral nutrients such as N, or that it had an intrinsic inability to use the excess nutrients. When P concentration in the tissues reached 0.45% of the dry mass, net photosynthesis declined with added P, suggesting that it had reached toxic concentrations. Furthermore, P enrichment did not affect chlorophyll concentration, but the *a*/*b* ratio declined, as did the proportions of chlorophylls to phaeopigments. At the same time, the proportions of carotenoids to chlorophylls increased. These responses likewise suggested P toxicity. In P-enriched aerated and nonaerated conditions, anoxia greatly reduced the P accumulation in just three days. This was likely due to blockage of mitochondrial respiration. This was followed by a distinct net loss of P, suggesting membrane damage. The photosynthetic response to K was lower than that to P.

Adaptations

Jungermannia exsertifolia subsp. ***cordifolia*** (Figure 135-Figure 137, Figure 140) has been the subject of many studies on the effects of enhanced UV. This interest has resulted in part from the loss of ozone in the stratosphere. Ozone serves as a filter against UV radiation. Hence, when fluorine in the atmosphere destroys ozone, the UV reaching the Earth increases.

One of the leading researchers on the effects of UV-B radiation on bryophytes is Martínez-Abaigar. He and his coworkers have laid the foundation for this research. In particular, they have concentrated on aquatic bryophytes. At higher elevations, the atmosphere is thinner, permitting more UV-B radiation to reach the surface of the Earth. Hence, mountain stream bryophytes are at particular risk because they lack a thick cuticle to help reduce the UV-B light. Martínez-Abaigar *et al*. (2006) specifically named ***Jungermannia exsertifolia*** subsp. ***cordifolia*** (Figure 135-Figure 137, Figure 140) as a good bio-indicator species for UV-B levels. Fv/Fm ratio, the concentration of UV-absorbing compounds (especially if they are analyzed individually), and DNA damage are good indicator variables for UV damage.

Fabón *et al*. (2011) pursued the effects of UV radiation on DNA in bryophytes, using ***Jungermannia exsertifolia*** subsp. ***cordifolia*** (Figure 135-Figure 137, Figure 140). DNA damage was significantly greater in PAB (PAR + UV-A + UV-B) treatments than in P (only photosynthetically active radiation, PAR) or PA (PAR + UV-A) treatments, making this species a good biomarker for UV-B damage. Under PAB treatment, DNA damage increased in thymine dimers following a period of high Par plus UV. But after UV cessation and return of PAR only, there was a rapid and complete repair. The net result showed little damage to this liverwort, indicating it is well adapted to the levels of UV in the lab experiment.

Temperature can make a difference in the amount of UV damage because of the reduced metabolism at low temperatures. Núñez-Olivera *et al*. (2005) cultured

Jungermannia exsertifolia subsp. ***cordifolia*** (Figure 135-Figure 137, Figure 140) and ***Fontinalis antipyretica*** (Figure 69) at 2ºC for 78 hours with continuous radiation to determine whether acclimation to sun or shade affected the UV-B response. The ***F. antipyretica*** was more sensitive to UV-B, showing significant decreases in several physiological variables. The sensitivity was present in both sun and shade plants, with shade plants being more sensitive. ***Jungermannia exsertifolia*** subsp. ***cordifolia***, on the other hand, had no difference in effect in shade- vs sun-acclimated plants.

Soriano *et al*. (2019) likewise found that ***Jungermannia exsertifolia*** subsp. ***cordifolia*** (Figure 135-Figure 137, Figure 140) acclimates to UV radiation intensity. Its response differences between sun and shade plants were moderate compared to those of ***Marchantia polymorpha*** (Figure 138-Figure 139), but greater than those of ***Fontinalis antipyretica*** (Figure 69).

Figure 138. ***Marchantia polymorpha*** gemmae cups on a wet population. Photo by Rudolf Macek, with permission.

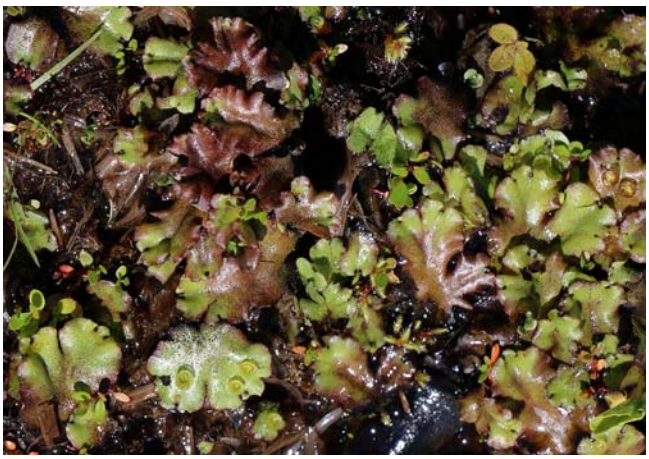

Figure 139. ***Marchantia polymorpha*** with red thallus, often a result of sun exposure. Photo by Paul Slichter, with permission.

Arróniz-Crespo *et al*. (2006) compared the responses of ***Jungermannia exsertifolia*** subsp. ***cordifolia*** (Figure 135-Figure 137, Figure 140) from mountain streams at a series of altitudes (1140-1816 m asl). They discovered two new caffeic acid derivatives, and the concentrations of these increased significantly with altitude. There was a significant linear relationship with altitude for additional measured parameters: MEUVAC (methanol-extractable UV-absorbing compounds), the maximal apparent electron transport rate through PSII (ETRmax), and the maximal non-photochemical quenching (NPQmax) all increased with altitude. Photoinhibition percentage decreased with altitude, suggesting that those populations from higher altitudes were exhibiting acclimation.

Martínez-Abaigar *et al.* (2009) likewise found evidence of acclimation to high UV radiation in populations of this species from high elevations. In their experiments, UV-B had little negative effect on photosynthetic performance or growth except in ***Jungermannia exsertifolia*** subsp. ***cordifolia*** (Figure 135-Figure 137, Figure 140). However, some pigments were affected negatively. UV-B protective compounds rarely increased (Figure 140). They attributed these muted responses to acclimation at their field altitudes of 1850-2000 m asl.

Figure 140. ***Jungermannia exsertifolia*** subsp. ***cordifolia*** on rock at edge of stream, emergent and underwater. Photo by Dick Haaksma, with permission.

Monforte *et al*. (2015a) similarly found little effect on Fv/Fm or DNA damage levels, hence making them inadequate as UV damage indicators. They supported the hypothesis of a strong acclimation capacity in ***Jungermannia exsertifolia*** subsp. ***cordifolia*** (Figure 135-Figure 137, Figure 140). On the other hand, coumarins were positively correlated with UV levels.

Martínez-Abaigar *et al*. (2003) found little response by ***Jungermannia exsertifolia*** subsp. ***cordifolia*** (Figure 135-Figure 137, Figure 140) to UV-A, but it did respond to UV-B. While the moss responded negatively in a number of measured parameters, the liverwort showed only a decreased Fv/Fm ratio, suggesting that this might be the most sensitive physiological variable. In addition, the concentration of UV-absorbing compounds increased with increased UV-B radiation.

Martínez-Abaigar *et al.* (2008) explored the effects of added phosphate on the UV-B response in ***Jungermannia exsertifolia*** subsp. ***cordifolia*** (Figure 135-Figure 137, Figure 140). They measured photosynthetic pigment composition, chlorophyll fluorescence, photosynthesis and respiration rates, and the accumulation of protecting UV-absorbing compounds – both the commonly used bulk UV-

absorbance of methanol extracts and the concentrations of five hydroxycinnamic acid derivatives in this liverwort. Although most of these variables were affected by the level of UV-B radiation, added phosphate had no significant effect on them except the vitality index (OD430/OD410) in the liverwort. They suggested that the liverwort has low nutrient requirements and that the added phosphate was stored as a luxury nutrient.

Monforte *et al*. (2015b) used 90 herbarium samples from Spain to assess usefulness of ***Jungermannia exsertifolia*** subsp. ***cordifolia*** (Figure 135-Figure 137, Figure 140) for UV radiation biomonitoring. They assessed both soluble (mostly vacuolar) and insoluble (bound in cell wall) UV-absorbing compounds. These provide a post-event means of assessment. For example, the soluble compound p-coumaroylmalic acid exhibited significantly higher concentrations after ~1975 when stratospheric ozone degradation was initiated. The bulk level of insoluble ultraviolet-absorbing compounds had the best spatial correlation with UV levels based on altitude and latitude. Summer and autumn samples differed significantly in both soluble and insoluble UV-absorbing compounds, reflecting the reduction of UV light in autumn in Spain.

Using a longer period of 82 days, Arróniz-Crespo *et al*. (2008) considered the response of five hydroxycinnamic acid derivatives to UV levels in ***Jungermannia exsertifolia*** subsp. ***cordifolia*** (Figure 135-Figure 137, Figure 140) from mountain streams. They found that the liverwort was tolerant to UV radiation, with the accumulation of three UV-absorbing hydroxycinnamic acid derivatives: p-coumaroylmalic acid, 5″-(7″,8″-dihydroxycoumaroyl)-2-caffeoylmalic acid, and 5″-(7″,8″-dihydroxy-7-O-β-glucosyl-coumaroyl)-2-caffeoylmalic acid being likely contributors to that tolerance. Thus, these three compounds are potential bioindicators of elevated UV levels.

Fabón *et al*. (2010) examined the effects of UV-B radiation on hydroxycinnamic acid derivatives from different cell compartments in ***Jungermannia exsertifolia*** subsp. ***cordifolia*** (Figure 135-Figure 137, Figure 140). They found a higher UV absorbance by the soluble fraction when compared to that of the cell-wall-bound fraction. Absorbance for both fractions increased when UV-B radiation was enhanced. The researchers identified five hydroxycinnamic acid derivatives in the soluble fraction and two more in the cell-wall-bound fraction. Of these, only p-coumaroylmalic acid in the soluble fraction and p-coumaric acid in the cell-wall-bound fraction increased under enhanced UV-B. DNA damage exhibited a strong increase under the enhanced UV-B, while the maximum quantum yield of PSII decreased.

Otero *et al*. (2006) assessed the effects of cadmium and enhanced UV radiation on ***Jungermannia exsertifolia*** subsp. ***cordifolia*** (Figure 135-Figure 137, Figure 140). Both caused degradation of chlorophyll and a decrease in the maximum quantum yield of photosystem II. At the same time, the xanthophyll index increased, permitting an increase in non-photochemical dissipation of energy. Cadmium elicited more stress than did the UV radiation, causing a decrease in net photosynthesis. UV radiation caused the level of trans-p-coumaroylmalic acid to increase, and cadmium caused trans-phaselic and feruloylmalic acids to increase. Elevated UV radiation alone resulted in DNA damage, and that was exacerbated when cadmium was elevated. This combined effect is probably a function of the ability of cadmium to inhibit DNA repair.

Fabón *et al*. (2012) found that PAB (PAR + UV-A + UV-B) samples increased in the bulk UV absorbance of both soluble and insoluble fractions; this response was most likely due, at least in part, to increases in the concentrations of p-coumaroylmalic acid in the soluble fraction and p-coumaric acid in the cell wall. They found seven hydroxycinnamic acid derivatives in the soluble and insoluble fractions. Most of these showed diel changes, responding within a few hours to radiation changes, but more strongly to UV-B. Significant and rapid changes occurred for Fv/Fm, ΦPSII, NPQ, and the components of the xanthophyll cycle in response to high PAR, UV-A, and UV-B radiation.

Núñez-Olivera *et al*. (2009) considered the seasonal variations in the UV-absorbing compounds and physiological changes with seasons in ***Jungermannia exsertifolia*** subsp. ***cordifolia*** (Figure 135-Figure 137, Figure 140). Using monthly collections for three years from a mountain stream, they found no DNA damage. The tender young shoots of summer-autumn with high Fv/Fm accumulated higher amounts of several hydroxycinnamic acid derivatives than did shoots collected in winter-spring. The p-coumaroylmalic acid proved to be the compound best associated with radiation changes.

Reproduction

Jungermannia exsertifolia subsp. ***cordifolia*** is **dioicous** and lacks gemmae (Smith 1990), suggesting that fragmentation may be an important means of reproduction.

Biochemistry

In addition to studies on compounds that protect against high light intensity and elevated UV radiation, there have been studies on other secondary compounds in ***Jungermannia exsertifolia*** subsp. ***cordifolia*** (Figure 135-Figure 137, Figure 140). Cullmann *et al*. (1999) found the typical liverwort **lignans** (any of class of polyphenolic compounds and noted for having antioxidant and estrogenic activity) and added three new ones. Nagashima *et al*. (1996) found eight new diterpenoids, added to the seven previously known. These have known biological activity against various cancer cell lines, plant-growth regulating properties, phytotoxic activity on root growth, as well as antiplasmodial, hypoglycemic, hypolipidemic, antimicrobial, antiviral, antifouling, larvicidal, algicidal, and insect antifeedant activities (Banerjee *et al*. 2008; Li *et al*. 2016; Lin-Gen *et al*. 2016; Pal *et al*. 2016; Bao *et al*. 2017; Li *et al*. 2017). They help to explain how a slow-growing liverwort can compete with bigger plants and ward off hungry insects.

To these, Scher *et al*. (2010) added a new diterpene derivative from this liverwort and found three previously known compounds. All of these demonstrated noticeable activity against a virulent tuberculosis pathogen.

Jungermannia pumila (Figure 141-Figure 143)

(syn. = *Aplozia pumila*, *Jamesoniella ruttneri*, *Solenostoma pumila*)

Distribution

Jungermannia pumila (Figure 141-Figure 143) is distributed in Europe, Asia, and North America (ITIS 2020j).

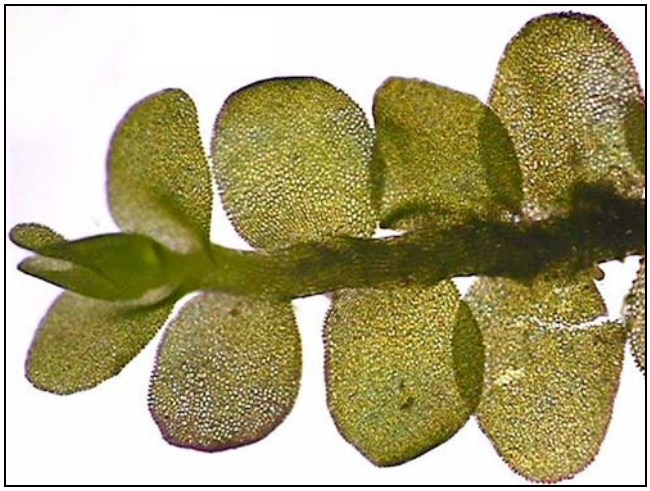

Figure 141. ***Jungermannia pumila***, a Northern Hemisphere species that can be found in some fast streams and deep in ponds. Photo by Paul Davison, with permission.

Figure 142. ***Jungermannia pumila***. Photo by Rambryo, through Creative Commons.

Figure 143. ***Jungermannia pumila*** forming a mat. Photo by Rambryo, through Creative Commons.

Aquatic Wet Habitats

Watson (1919) attributed ***Jungermannia pumila*** (Figure 141-Figure 143) to rocks or gravel associated with fast streams, waterfalls, more aquatic in fast streams. Ruttner (1955) reported it submersed in a pond and <40 cm above water level in the tropics. Philippi (1987) considered it rare in aquatic habitats of eastern Odenwald and southern Spessart, Germany. Marstaller (1987) noted its occurrence in the ***Platyhypnidium*** (Figure 68)-***Fontinalis antipyretica*** (Figure 69) association in Thuringia, Germany. Heino and Virtanen (2006) affirmed its occurrence in streams in northeastern Finland. And Luis *et al*. (2015) found it in mountainous streams on Madeira Island. In the UK, ***J. pumila*** (Figure 141-Figure 143) usually grows on damp rock on cliffs, low rock outcrops in woodlands, or low down on rock faces by rivers; sometimes it occurs on soil (BBS 2020).

Adaptations

Like many of the species in this genus, ***Jungermannia pumila*** (Figure 141-Figure 143), this species is small and exhibits a dull green to blackish coloration (Smith 1990). Unlike many of the wet-habitat species in this genus, it produces numerous rhizoids. It often grows with other bryophytes, a behavior that can help it to maintain moisture.

Reproduction

Jungermannia pumila (Figure 141-Figure 143) is **paroicous** and perianths (Figure 144) are common (Smith 1990; Hodgson 2021). Capsules are likewise common, produced in winter and spring. Gemmae are absent.

Figure 144. ***Jungermannia pumila*** fertile branches with females in center and male bracts below them. Photo by Andrew Hodgson, with permission.

Jungermannia quadridigitata

(syn. = *Lepidozia setacea*, *Microlepidozia setacea*)

Distribution

Jungermannia quadridigitata is listed by Söderström *et al*. (2016) as being of serious doubt. It is possible it is now included in one of the other taxa listed here. For this reason, I am unable to provide distribution information.

Aquatic and Wet Habitats

The species is not a true aquatic, but occurs in moist hollows between ***Sphagnum*** hummocks (Figure 145) on Cape Breton Island, Canada (Nichols 1918). Weber (1976) also included it among bog bryophytes in Cataracts Provincial Park, Newfoundland, Canada, considering it a typical bog bryophyte.

Figure 145. Raised bog with ***Sphagnum fimbriatum*** surrounded by ***Sphagnum magellanicum***, where ***Jungermannia quadridigitata*** can occur in the hollows between hummocks like these. Photo through Creative Commons.

Mesoptychia badensis (Figure 146-Figure 148, Figure 150)

(syn. = *Lophozia badensis*)

Distribution

Mesoptychia badensis (Figure 146-Figure 148, Figure 150) is listed by TROPICOS for China and Russia. Crandall-Stotler *et al*. (2013), however, considered it to be widely distributed in the northern hemisphere.

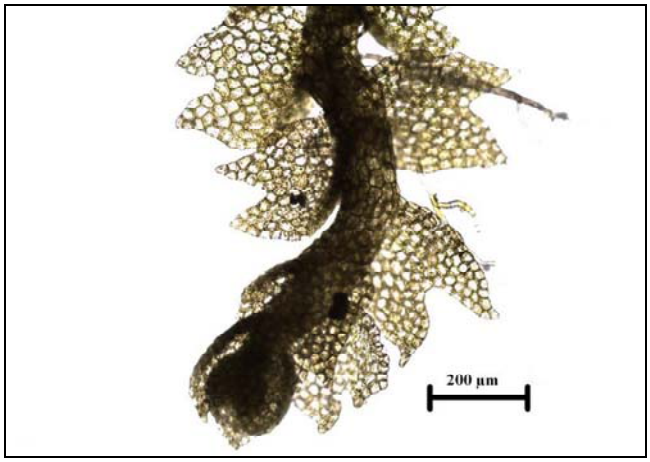

Figure 146. ***Mesoptychia badensis***, a species widely distributed in the Northern Hemisphere in calcareous habitats, including streams and rivers. Photo by Hugues Tinguy, with permission.

Figure 147. ***Mesoptychia badensis***. Photo by Štěpán Koval, with permission.

Aquatic and Wet Habitats

Nichols (1916) reported this species from calcareous rivers in Connecticut, USA. Watson (1919) treated it as occasionally submerged. In the Lorraine River, Belgium, it occurred in the travertine ***Cratoneuron*** (Figure 149) association (de Sloover & Goossens 1984). Bakalin *et al*. (2019a) found the species in the krummholz and tundra-like habitats where it grew in open wet to mesic limestone cliff crevices and on fine limestone deposits near small streams in the Balagan Mountain and Vengeri River Valley (Sakhalin Island, North-West Pacific).

Figure 148. ***Mesoptychia badensis***. Photo by Štěpán Koval, with permission.

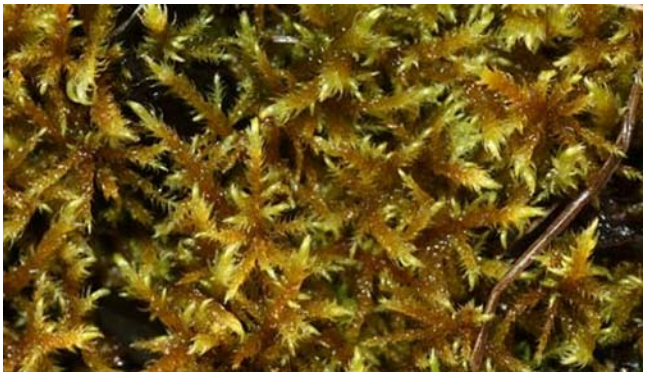

Figure 149. ***Cratoneuron filicinum***; ***Mesoptychia badensis*** occurs in association with ***Cratoneuron*** in the travertine. Photo by Barry Stewart, with permission.

Reproduction

The species is **dioicous**, but at least sometimes produces capsules (Figure 150). On the other hand, it does not produce gemmae (Potemkin *et al*. 2015). We should look for its ability to reproduce from fragments, especially in the field. This could be especially important in rivers, streams, and areas subject to flooding.

Figure 150. ***Mesoptychia badensis*** with capsules, despite being dioicous. Photo by Štěpán Koval, with permission.

Mesoptychia bantriensis (Figure 151-Figure 153)

(syn. = *Leiocolea bantriensis*)

Distribution

Mesoptychia bantriensis (Figure 151-Figure 153) occurs in Europe, Asia, and North America (Bakalin 2018). Hodgetts (2015) listed it specifically from Norway, Sweden, United Kingdom, and Italy in Europe.

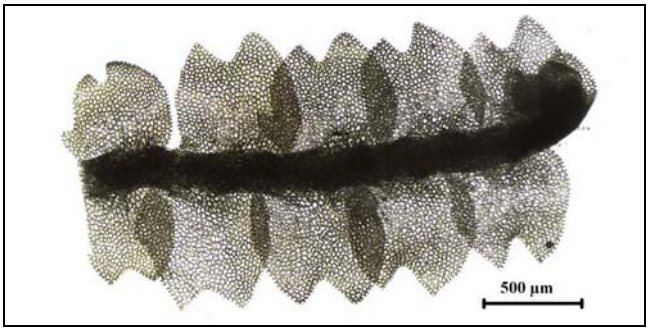

Figure 151. ***Mesoptychia bantriensis***, a Northern Hemisphere liverwort of streams, rivers, lakes, and their banks, as well as mires and moist tundra. Photo by Hugues Tinguy, with permission.

Figure 152. ***Mesoptychia bantriensis*** showing growth habit. Photo by Štěpán Koval, with permission.

Aquatic and Wet Habitats

Watson (1919) listed this species as one of alpine and subalpine rocks and on soil by fast water. Heino and Virtanen (2006) reported it from streams in northeastern Finland. Bakalin *et al*. (2016) reported it from moist soil or on mineral ground of mesic tundras, but also along streams and on lake shores, on cliffs near waterfalls, on peat in mires, on peat in minerotrophic bogs, on silty alluvium along lake shores, and on fine soil and humus along watercourses on the Putorana Plateau in East Siberia. It forms mats on its substrate (Figure 153).

Adaptations

Mesoptychia bantriensis (Figure 151-Figure 153) forms green to reddish-brown tufts and patches (Smith 1990). This coloration can be beneficial in locations where it is exposed to bright light and low temperatures at the same time by protecting it from photoinhibition.

Figure 153. ***Mesoptychia bantriensis*** showing mat formation. Photo by Barry Stewart, with permission.

Reproduction

Mesoptychia bantriensis is **dioicous** and lacks gemmae (Smith 1990). Perianths can be seen only occasionally and capsules are rare.

Mesoptychia collaris (Figure 154)

(syn. = *Leiocolea collaris*, *Lophozia muelleri*)

Distribution

Mesoptychia collaris (Figure 154) occurs in Europe, Asia, Africa, and North America (ITIS 2019).

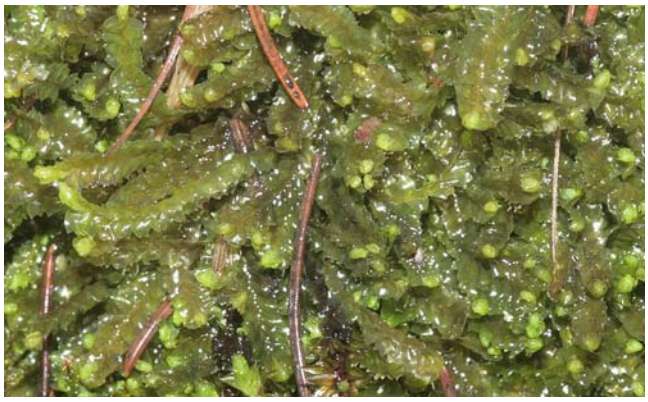

Figure 154. ***Mesoptychia collaris***, a Northern Hemisphere species that is hemicalciphilous in cold streams and seepage areas. Photo by Hermann Schachner, through Creative Commons.

Aquatic and Wet Habitats

Mesoptychia collaris (Figure 154) was considered by Watson (1919) to occur on alpine and subalpine rocks by fast water. In western Canada it is submerged in montane streams where it is hemicalciphilous (Vitt *et al*. 1986; Glime & Vitt 1987). In Thuringia, Germany, it occurred in the ***Platyhypnidium*** (Figure 68)-***Fontinalis antipyretica*** (Figure 69) association (Marstaller 1987). In the Tara river canyon and Durmitor area of Montenegro it occurred at a spring and river (Papp & Erzberger 2011). Konstantinova and Lapshina (2014) considered it to be calciphilous in seepage areas on schists on a steep rocky slope to the valley of a rivulet in the eastern subpolar Urals in Russia.

Adaptations

Mesoptychia collaris (Figure 154) forms green to brown patches (Smith 1990), suggesting the possibility of protection from high light intensities. It often grows through patches of other bryophytes, providing a greater opportunity to maintain moisture.

Reproduction

Mesoptychia collaris (Figure 154) is **dioicous** (Smith 1990). Perianths occur only occasionally and capsules are rare. Gemmae are absent.

Mesoptychia gillmanii (Figure 155)

(syn. = *Leiocolea gillmanii*)

Distribution

Mesoptychia gillmanii (Figure 155) is widespread around the northern hemisphere in boreal and montane regions, although it is considered vulnerable in Europe (Hodgetts *et al*.).

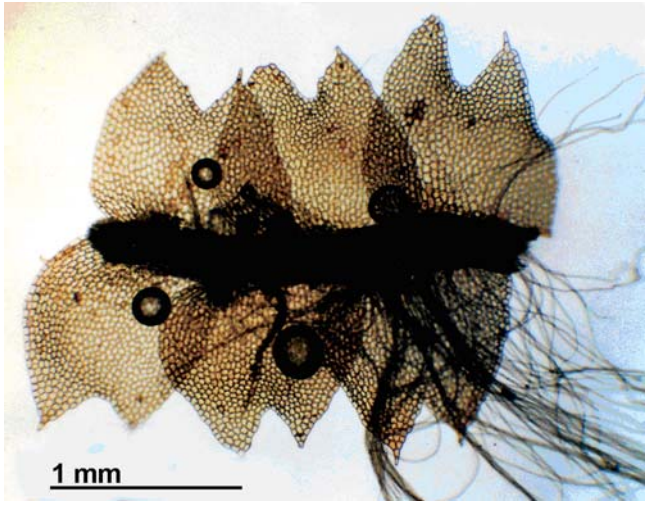

Figure 155. ***Mesoptychia gillmanii***, a species from boreal and montane regions of the northern hemisphere. It is a calciphile in streams, on peaty soil, and on cliffs and ledges. Photo by David Wagner, with permission.

Aquatic and Wet Habitats

In Finland, ***Mesoptychia gillmanii*** (Figure 155) occurs in streams (Heino & Virtanen 2006). In North America, this species is found on peaty soil, typically on cliffs or ledges. Nevertheless, it is an obligate calciphile (Schuster 1969). The species often occurs at elevations where the snow leaves late in the growing season, giving it a short growing season.

Adaptations

Mesoptychia gillmanii (Figure 155) lacks the coloration seen by many members of this family, instead displaying only green to yellowish-green coloration (Smith 1990). Like many members of the family, it grows among other bryophytes, a behavior that can help it to maintain moisture.

Reproduction

Mesoptychia gillmanii (Figure 155) is a perennial that, like most members of the genus, produces no gemmae. This means its dispersal must be primarily by spores or fragments (Wagner 2018). It is, however, **paroicous (Smith 1990)**, increasing the potential for fertilization and spore production.

Mesoptychia turbinata (Figure 156-Figure 157)

(syn. = *Lophozia turbinata*)

Distribution

Mesoptychia turbinata (Figure 156-Figure 157) is apparently restricted to the Mediterranean area of Europe and North Africa (Schuster 1969).

Aquatic and Wet Habitats

Watson (1919) considered ***Mesoptychia turbinata*** (Figure 156-Figure 157) to be a species on stream banks that experience frequent submergence and to occasionally be submerged. Papp *et al*. (2018) reported it from limestone rock at a rivulet in Albania. This species is a calcicole and does best in a *p*H range of 4-8 with 3.0 mM Ca^{++} (Jefferies 1969). The K^{+} efflux appears to be unaffected by the Ca^{++} concentration in this species.

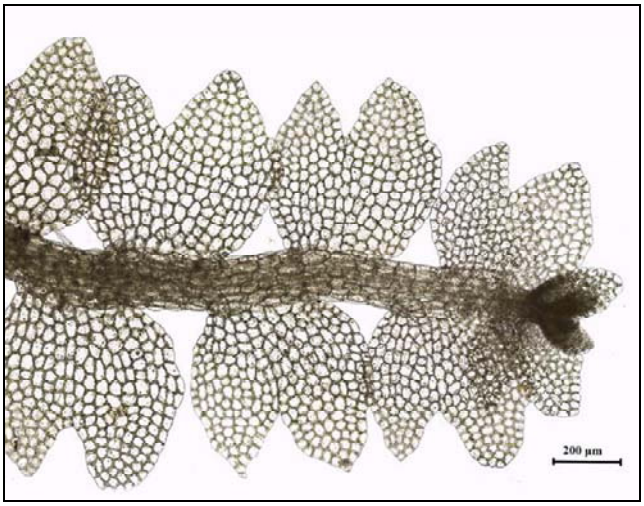

Figure 156. ***Mesoptychia turbinata***. Photo by Hugues Tinguy, with permission.

Adaptations

Like the previous species, ***Mesoptychia turbinata*** (Figure 156-Figure 157) lacks the protective reds and browns that might protect it from exposure to bright light. Instead, its coloration ranges from pale green to yellowish-green (Figure 157). It most likely gains moisture retention

where it grows among other bryophytes. or through its rather dense mats (Figure 157).

Figure 157. ***Mesoptychia turbinata*** showing the extensive mats that are possible. Photo by Hugues Tinguy, with permission.

Reproduction

Mesoptychia turbinata (Figure 156-Figure 157) is **dioicous**, but nevertheless produces frequent perianths in the UK (Smith 1990). Capsules, however, are only occasional, appearing in winter or spring in the UK.

Notoscyphaceae

Notoscyphus lutescens (Figure 158)

(syn. = *Notoscyphus paroicus*)

Distribution

Notoscyphus lutescens (Figure 158) occurs in the Western Ghats (Udar & Kumar 1981; Singh *et al*. 2016) and in Hong Kong and mainland China, sometimes on wet soil (So & Zhu 1996). It extends into the southern hemisphere to New Zealand (Braggins *et al*. 2014), and is known from South Africa, Madagascar, India, China, Japan, Philippines, Indonesia, Papua New Guinea, north-eastern Australia (Queensland), as well as New Caledonia, Hawaii, Fiji, and Samoa (Schuster 2002). Not surprisingly, it has more recently been found in Australia.

Figure 158. ***Notoscyphus lutescens***, an Eastern Hemisphere species, occurring where it is aquatic or wetland, including river banks and seeping cliffs. Photo by David Tng, with permission.

Aquatic and Wet Habitats

Ruttner (1955) reported ***Notoscyphus lutescens*** (Figure 158) as an aquatic or wetland species in the tropics. In Malawi, O'Shea *et al*. (2001) found it on river banks and on both dry and moist granitic and sandstone rocks, among other terrestrial habitats. Pócs and Streimann (2006) reported it from a riverside earth bank in Australia. Omar *et al*. (2016) documented it from a wetland in South Africa. It is also known from a seeping cliff at 900 m in the Nguru Mountains of Tanzania (Pócs & Váňa 2015).

Reference to aquatic habitats are rare or non-existent among the reports on its localities. Nevertheless, this species is sold in some areas as an aquarium plant <https://aquaticarts.com/, Brownsburg, IN, USA>.

Adaptations

Members of ***Notoscyphus*** are typically yellowish-green, but can become red with age (Winterton *et la*. 2018).

Reproduction

Notoscyphus lutescens (Figure 158) is dispersed by spores and stem fragments (Winterton *et al*. 2018).

Biochemistry

Wang *et al*. (2014) reported ten new diterpenoids from this species. One of the compounds exhibited activity against human prostate cancer cells. So and Chan (2001) found a new cyclic bis (bibenzyl) derivative with activity against bacteria *Bacillus subtilus* (Figure 159) and two strains of *Staphylococcus aureus* (Figure 160). Zhu *et al*. (2006) found antibacterial activity against all five bacteria they tested, but were unable to find any oil body characters that were linked statistically to antibiotic activity. It is likely that some of these compounds are also inhibitory to environmental pathogens.

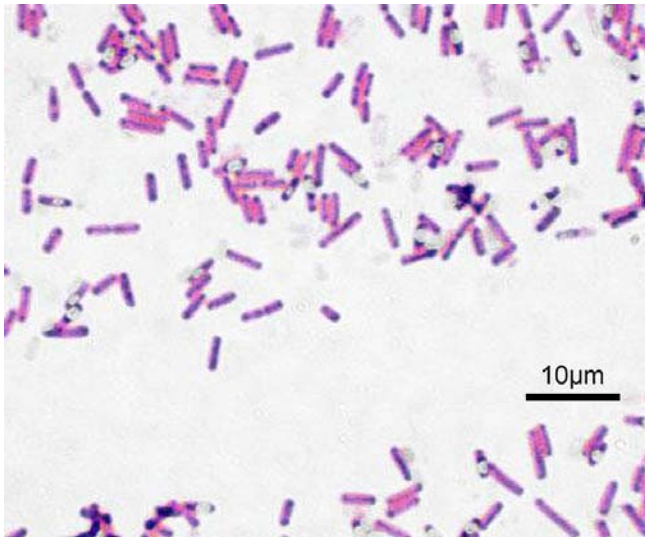

Figure 159. ***Bacillus subtilis*** with Gram stain, a species that is inhibited by extracts of ***Notoscyphus lutescens***. Photo by Y. Tambe, through Creative Commons.

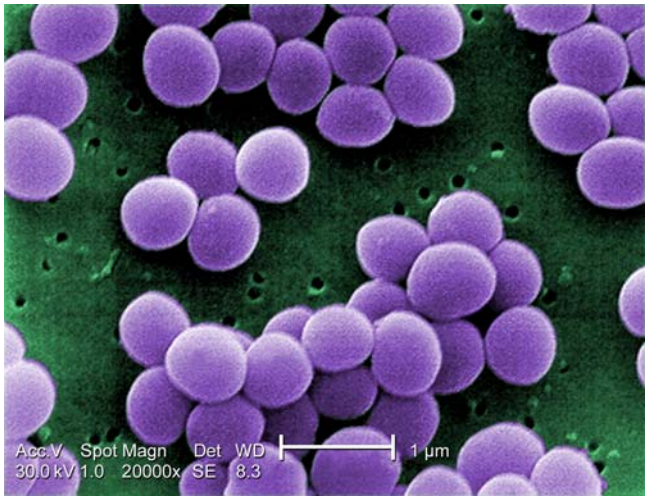

Figure 160. ***Staphylococcus aureus***, a species that is inhibited by extracts of ***Notoscyphus lutescens***. Photo by Janice Haney Carr, through public domain.

Figure 162. ***Saccogyna viticulosa*** with branches in a semi-upright position. Photo by Dick Haaksma, with permission.

Saccogynaceae

Saccogyna viticulosa (Figure 161-Figure 163)

Distribution

Saccogyna viticulosa (Figure 161-Figure 163) is listed for Europe, Africa, and Asia by ITIS (2020k). Mateo *et al*. (2013) treat it as a hyper-oceanic species along the Atlantic Ocean. Kürschner (2010) added it to southwest Asia, describing its previous known distribution as western Mediterranean and Atlantic region.

Figure 163. ***Saccogyna viticulosa*** forming a mat. Photo by Dick Haaksma, with permission.

Figure 161. ***Saccogyna viticulosa***, a species mostly along the eastern side of the Atlantic Ocean where it is wet for long periods or even submerged. Photo by Dick Haaksma, with permission.

Aquatic and Wet Habitats

This species is one occurring with high humidity, sometimes being wet for long periods of time or even submerged. In northwestern Portugal, ***Saccogyna viticulosa*** (Figure 161-Figure 163) occurs in small crevices with humus and high humidity in the stream or waterfall margins that may be subjected to inconstant splashes or inundation. It is never extensive, always mixed with other bryophytes, often associated with ***Pellia epiphylla*** (Figure 164), ***Fissidens polyphyllus*** (Figure 103), ***Hyocomium armoricum*** (Figure 165-Figure 166), ***Plagiothecium nemorale*** (Figure 167), and ***Riccardia multifida*** (Figure 168) in wetter situations, with ***Radula holtii*** in dripping conditions, and in mountain streams (Vieira *et al.* 2004, 2005). In the Laurel forest of the Canary Islands, it occurs on periodically moistened, rather exposed volcanic rocks (Dirkse 1985). On Madeira Island, it occurs in low altitude, narrow streams and low flow in mountainous

streams (Luis *et al.* 2015). In the British Isles, it occurs in many small, rocky streams (Averis & Hodgetts 2013).

Figure 164. ***Pellia epiphylla*** showing an associated leafy liverwort. Photo by Jan-Peter Frahm, with permission.

Figure 165. ***Hyocomium armoricum*** habitat such as those where we might find ***Saccogyna viticulosa*** in association. Photo by Dick Haaksma, with permission.

Figure 166. ***Hyocomium armoricum***, sometimes an associate of ***Saccogyna viticulosa***. Photo by Michael Lüth, with permission.

Figure 167. ***Plagiothecium nemorale***, sometimes an associate of ***Saccogyna viticulosa***. Photo by Hermann Schachner, through Creative Commons.

Figure 168. ***Riccardia multifida*** showing its habitat with a leafy liverwort on the right. Photo by Rick Ballard, through Creative Commons.

In northwestern Portugal, ***Saccogyna viticulosa*** (Figure 161-Figure 163) was never extensive and always occurred in mixtures with other bryophytes – a behavior suggesting its need for constant moisture (Vieira *et al.* 2004). However, in experiments, ***Saccogyna viticulosa*** had survival down to 51% relative humidity with only a few cells surviving down to 33% relative humidity (Clausen 1964). It is likely that it would have even greater survival in nature where the drying time would be more extended, permitting the cells to prepare (*e.g.* Stark *et al.* 2013). At -10ºC in ice, undeveloped apical cells died within 1-2 days. In other experiments, Proctor (2010) showed that ***Saccogyna viticulosa*** cells are easily damaged by bright light during initial rewetting. Dilks and Proctor (1974) found that despite the rapid damage and slow recovery of assimilation, this species has the capacity to survive long dry periods. At the beginning of rehydration, dark respiration typically shows a slight stimulation, followed by a longer-term buildup after a moderate or prolonged desiccation. Pressel *et al.* (2009) found that this species can withstand several weeks of natural drying. The estimated recovery time is 0.4 hours. The species typically occurs in shaded sites where they probably are never subject to intense desiccation. Of the species tested in this study, ***Saccogyna viticulosa*** (Figure 161-Figure 163) lives

in niches with the lowest irradiance and least severe desiccation, especially avoiding direct summer sun.

Reproduction

One reason for the scarcity of ***Saccogyna viticulosa*** (Figure 161-Figure 163) in some areas is its **dioicous** habit, limiting spore production (Watson & Dallwitz 2019). In northwestern Portugal, Vieira *et al*. (2004) never found the species fertile. This problem is compounded by the absence of gemmae, at least in the UK (Watson & Dallwitz 2019).

Fungal Interactions

Wang and Qiu (2006) reported fungal associations with this species. ***Saccogyna viticulosa*** (Figure 161-Figure 163) is known to host the fungus ***Sebacina*** (Figure 169) (Bidartondo & Duckett 2010). It produces numerous hyphae associated with the branched rhizoid apex. Döbbeler (2011) found that the **Ascomycete** fungus ***Octosporella fortunata*** occurs on terricolous populations of ***Saccogyna viticulosa*** on the Canary Islands. This fungus produces its spores in sacs that are hidden within the mats of liverworts. Ing (1983) found **Myxomycetes** to be frequently associated with ***Saccogyna viticulosa*** in wooded ravines in Highland Britain.

Figure 169. ***Sebacina incrustans***, in a genus that is known from ***Saccogyna viticulosa***, shown here on a moss. Photo through Creative Commons.

Biochemistry

Several biochemical studies have revealed the array of secondary compounds in ***Saccogyna viticulosa*** (Figure 161-Figure 163). Suleiman *et al*. (1980) demonstrated that even photosynthetic products in this species may differ from that in other families that have been considered closely related. Connolly *et al*. (1994) found two new sesquiterpenoids in ***Saccogyna viticulosa***. Hackl *et al*. (2004) identified several new sesquiterpenes from populations on Madeira and unravelled some of the pathways involved in making the volatile essential oils in this species.

Solenostomataceae

Solenostoma (Figure 170-Figure 176, Figure 177-Figure 189, Figure 193-Figure 196)

Solenostoma (Figure 170-Figure 176, Figure 177-Figure 189, Figure 193-Figure 196) has **psychrorithral** (cold upper stream reaches) species in European alpine streams (Geissler 1975).

Solenostoma ariadne

(syn. = *Nardia ariadne*)

Solenostoma ariadne is known from India and China. Ruttner (1955) reported it as a wetland/aquatic species from the tropics.

Solenostoma gracillimum (Figure 170-Figure 172)

(syn. = *Jungermannia gracillima* fo. *crenulata*, *Solenostoma crenulatum*)

Distribution

Solenostoma gracillimum (Figure 170-Figure 172) is known from Europe, Asia, Africa, North America, and South America (ITIS 2020l).

Figure 170. ***Solenostoma gracillimum***, a species known from both the Northern and Southern Hemispheres, living in streams, small lakes, and in other wet areas. Photo by Hugues Tinguy, with permission.

Figure 171. ***Solenostoma gracillimum*** showing its growth habit. Photo by David T. Holyoak, with permission.

Aquatic and Wet Habitats

Most of the wet habitat reports are relatively recent. Bley (1987) reported ***Solenostoma gracillimum*** (Figure 170-Figure 172) from upstream reaches in the Harz Mountains of Germany. Toivonen and Huttunen (1995) found it in small lakes in southern Finland. It occurs in mountain streams of northwest Portugal (Vieira *et al.* 2005) and in Madeira Island (Luis *et al.* 2015). Ferreira *et al.* (2008) listed it for European rivers. In North America its wet habitats include ditches and ravine walls (Breil 1970).

The plants become reddish (Figure 172) when exposed to the sun (Breil 1970).

Figure 172. ***Solenostoma gracillimum*** showing red coloration often seen with sun exposure. Photo by Barry Stewart, with permission.

Solenostoma gracillimum (Figure 170-Figure 172) is one of the species that can facultatively live in areas with metalliferous mine waste (Holyoak 2008). In Ireland, it was indicative of copper waste, but it does not require excess copper to colonize. This is a habitat where drying would appear to be frequent.

Solenostoma gracillimum (Figure 170-Figure 172) seems to have an unusual tolerance for zinc. In the Hautes-Pyrénées, this species was one of only three present where Zn had reached such high concentrations that it formed a white precipitate of **anglesite** (Figure 173), along with ***Pohlia cruda*** (Figure 174) and ***Schizothrix*** sp. (Figure 175) (Say & Whitton 1982). Similarly, Brown and House (1978) found it growing near a lead mine and on spoil from a copper mine in southwest England.

Figure 173. Anglesite, a rock type that can precipitate onto bryophytes. Photo by Parent Géry, through Creative Commons.

Figure 174. ***Pohlia cruda***, a species that occurs with ***Solenostoma gracillimum*** in areas with high levels of zinc. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission from Russ Kleinman and Karen Blisard.

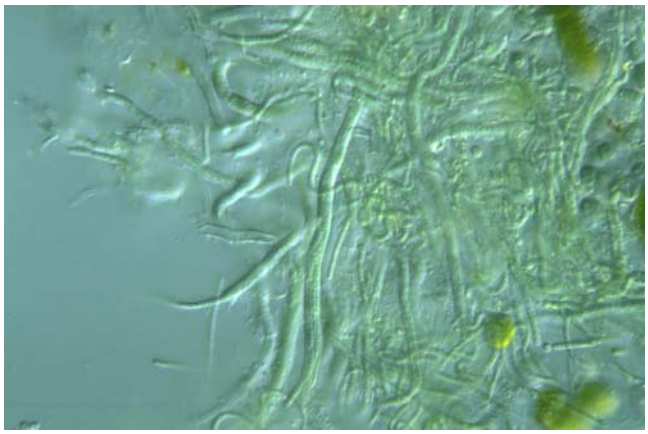

Figure 175. ***Schizothrix*** sp., member of a genus that occurs with ***Solenostoma gracillimum*** in areas with high levels of zinc. Photo by Yuuji Tsukii, with permission.

Reproduction

Solenostoma gracillimum (Figure 170-Figure 172) is **dioicous** (Figure 176) (Breil 1970), but has a widespread distribution that suggests that at least some spores have dispersed. It does not produce gemmae (Bakalin 2012).

Figure 176. ***Solenostoma gracillimum*** with numerous perianths. Photo by David T. Holyoak, with permission.

Fungal Interactions

Solenostoma gracillimum (Figure 170-Figure 172) is one of the hosts of the fungus ***Mniaecia jungermanniae*** (Figure 24-Figure 26) (Egertová *et al*. 2016). Pressel and Duckett (2006) found that it infected some liverwort species, but not others.

Solenostoma hyalinum (Figure 177-Figure 179)

(syn. = *Eucalyx hyalina*, *Jungermannia hyalina*)

Distributions

Solenostoma hyalinum (Figure 177-Figure 179) is widespread in Europe, south to northern Africa, but up to 1969 only one Asian country had a recorded species (Schuster 1969). It occurs in North America from Quebec, Canada, southward to North Carolina, USA, and westward through the Midwest to Mexico.

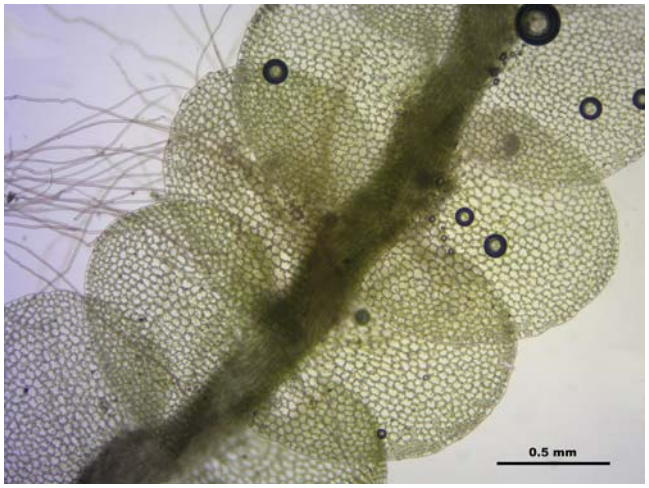

Figure 177. ***Solenostoma hyalinum***, a Northern Hemisphere species that lives where it is constantly wet or submerged. Photo by Hermann Schachner, through Creative Commons.

Figure 178. ***Solenostoma hyalinum***, a Northern Hemisphere species that lives where it is constantly wet or submerged. Photo by Hermann Schachner, through Creative Commons.

Solenostoma hyalinum (Figure 177-Figure 179) in North America occurs primarily at median and low elevations (Schuster 1969). Although it has rare occurrences in the taiga, it does not reach higher elevations in the southeastern states of the USA. It is able to form extensive mats on river banks. Schuster has never observed it any considerable distance from streams. It seems to require at least some soil, not occurring on bare rocks.

Early in aquatic studies, Watson (1919) reported ***Solenostoma hyalinum*** (Figure 177-Figure 179) as a species that is occasionally submerged. But others have documented a wider and wetter range of habitats. Vieira *et al*. (2004, 2005), based on their studies in northwest Portugal, reported it from vertical faces of boulders subjected to splashes or constant drippings and in the margins of waterfalls, associated with ***Scapania undulata*** (Figure 60), ***Hyocomium armoricum*** (Figure 165-Figure 166), ***Fissidens polyphyllus*** (Figure 103), and ***Platyhypnidium lusitanicum*** (Figure 104), as well as in mountain streams. Ferreira *et al*. (2008) reported it from rivers. It occurs in mountain streams on Madeira Island (Luis *et al.* 2015). Duckett and Slack (2013) found it on vertical wet rocks in Tuckerman Ravine on Mt. Washington, New Hampshire, USA. Hong (1972) reports the species from several streams in Montana, USA. Weber (1976) considered it to be a river bank species in the Cataracts Provincial Park, Newfoundland, Canada. Likewise, Kitagawa (1978a) found it on river banks where it can form large, compact mats on rocks.

Reproduction

In northwest Portugal, ***Solenostoma hyalinum*** (Figure 177-Figure 179) has only been found sterile in pure or mixed well-developed patches (Vieira *et al*. 2004). Nevertheless, it can produce capsules (Figure 179) when both genders are present.

Figure 179. ***Solenostoma hyalinum*** with a capsule, indicating that some populations can successfully reproduce sexually. Photo by Michael Lüth, with permission.

Fungal Interactions

Solenostoma hyalinum (Figure 177-Figure 179) is one of the known hosts for the Ascomycete fungus ***Mniaecia jungermanniae*** (Figure 24-Figure 26) (Egertová *et al*. 2016). The exact relationship needs to e explored.

Solenostoma inundatum (Figure 180-Figure 181)

(syn. = *Jungermannia inundata*)

Distribution

Solenostoma inundatum (Figure 180-Figure 181) occurs in Australia and New Zealand (Allison & Child 1975; ITIS 2121).

Figure 180. ***Solenostoma inundatum***, a species from Australia and New Zealand. Photo owned by the University of Auckland, with online permission for educational use.

Figure 181. ***Solenostoma inundatum***, a species that can be found in some mountain streams. Photo owned by the University of Auckland, with online permission for educational use.

Aquatic to Wet Habitats

Solenostoma inundatum (Figure 180-Figure 181) occurs on soil or rocks in wide-ranging habitats from mountain streams to dry pumice banks (Allison & Child 1975). Its name implies that it lives where it can at least some of the time become submersed. Scott (1985) described it as occurring on wet clay banks in wet sclerophyll forest where it is a common pioneer. It often occurs with other bryophytes, especially ***Jackiella*** and ***Isotachis.***

Figure 182. ***Jackiella javanica***, a liverwort that frequently serves as a substrate for ***Solenostoma inundatum***. Photo from Taiwan Mosses Color Illustrations, through Creative Commons.

Figure 183. ***Isotachis*** sp., a liverwort that frequently serves as a substrate for ***Solenostoma inundatum***. Photo by Phil Bendle, with permission through John Grehan.

Adaptations

When submersed, the plants of ***Solenostoma inundatum*** (Figure 180-Figure 181) are bright green, but when on exposed banks they are bright red (Allison & Child 1975). The red coloration is most likely induced by the bright light in exposed sites and can protect for UV damage, especially when dry.

Reproduction

The sexual status of ***Solenostoma inundatum*** (Figure 180-Figure 181) is unclear, with Scott (1985) listing it as

dioicous and Bakalin (2014) listing at as **dioicous** with a question mark. Smaller plants produce bright pink perianths (Figure 184) that can at times be quite numerous (Allison & Child 1975). The capsules mature (Figure 185) and dehisce with spiral cleavage (Figure 186).

Figure 184. ***Solenostoma inundatum*** with perianth. Photo owned by the University of Auckland, with online permission for educational use.

Figure 185. ***Solenostoma inundatum*** capsule. Photo owned by the University of Auckland, with online permission for educational use.

Figure 186. ***Solenostoma inundatum*** dehiscing capsule. Photo owned by the University of Auckland, with online permission for educational use.

Solenostoma javanicum

(syn. = *Aplozia javanica*)

Solenostoma javanicum occurs in Australia and southern Asia (ITIS 2020m). The only report of a wet habitat I could find was that of Ruttner (1955). He reported it from sulfur springs in the tropics.

Solenostoma obovatum (Figure 187)

(syn. = *Eucalyx obovata*, *Eucalyx obovata* fo. *elegatus*, *Eucalyx obovata* fo. *laxus*, *Eucalyx obovata* var. *rivularis*, *Jungermannia obovata*, *Nardia obovata*, *Plectocolea obovata*)

Distribution

Solenostoma obovatum (Figure 187) occurs sparingly in the Arctic, then southward in the mountains of Europe and North America (Schuster 1969).

Figure 187. ***Solenostoma obovatum***, a species from the Arctic southward to the mountains of Europe and North America, occurring in rivers and streams and on their banks. Photo by Michael Lüth, with permission.

Aquatic and Wet Habitats

An early report by Nichols (1918) attributed ***Solenostoma obovatum*** (Figure 187) to a rock ravine streambank, Cape Breton Island, Canada (Nichols 1918). Watson (1919) reported it from rocks or soil of fast streams, usually on submerged rocks, and on banks with frequent submergence and slow water. In the mountains of Westfalens, northwestern Germany, it occurs in shallow water (Koppe 1945). But others attribute it to more aquatic habitats. It occurs in alpine streams in the Swiss Alps (Geissler 1976). In Thuringia, Germany, it occurs in the ***Platyhypnidium*** (Figure 68)***-Fontinalis antipyretica*** (Figure 69) association (Marstaller 1987). And it occurs in the Iskur River, Bulgaria, and its main tributaries (Papp *et al*. 2006). Light (1975) reported a species he questionably attributed to ***Solenostoma cf. obovatum*** from small lakes in Scottish mountains with ice cover 4-7 months per year and low ion concentrations.

Reproduction

Solenostoma obovatum (Figure 187) is **paroicous** (Schuster 1969). It apparently lacks gemmae, as is typical for this family.

Solenostoma sphaerocarpum (Figure 188-Figure 189, Figure 193)

(syn. = *Aplozia sphaerocarpa*, *Haplozia sphaerocarpa*, *Jungermannia sphaerocarpa*)

Distribution

Solenostoma sphaerocarpum (Figure 188-Figure 189, Figure 193) occurs across Siberia and is known from Japan (Váňa *et al*. 2013). ITIS (2020n) lists Europe, Asia, Africa, Oceania, Australia, North America from Alaska to Mexico, and South America.

Figure 188. ***Solenostoma sphaerocarpum***, a worldwide species from streams and rivers and their banks. Photo by Hugues Tinguy, with permission.

Aquatic and Wet Habitats

Szweykowski (1951) reported ***Solenostoma sphaerocarpum*** (Figure 188-Figure 189, Figure 193) from moist stones and rocks in stream beds in the Gory Stolowe Mountains of Poland. Konstantinova and Vasiljev (1994) found it on rocks on a stream bank, mixed with ***Blepharostoma trichophyllum*** (Figure 190), ***Mesoptychia heterocolpos*** (Figure 191), ***Tritomaria scitula***, and ***Lophoziopsis excisa*** (Figure 192) in the Sayan Mountains of southern Siberia. Miller and Shushan (1964) reported it from stream banks in Oregon, USA. Geissler (1976) found it in alpine streams in the Swiss Alps. It occurs in the upper and middle reaches of streams in the Harz Mountains of Germany (Bley 1987), and in the ***Platyhypnidium*** (Figure 68)***-Fontinalis antipyretica*** (Figure 69) stream association in Thuringia, Germany (Marstaller 1987). Ferreira *et al*. (2008) considered it to be a species of rivers. Tremp and Kohler (1991) consider it to be a species of low-buffered water of streams.

Figure 189. ***Solenostoma sphaerocarpum*** showing its matted growth habit. Photo by Hugues Tinguy, with permission.

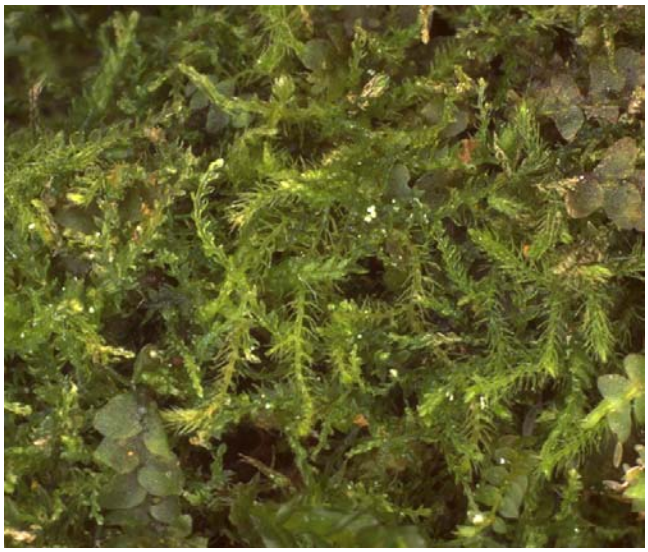

Figure 190. ***Blepharostoma trichophyllum***, an associate of ***Solenostoma sphaerocarpum*** on stream banks. Photo by Jan-Peter Frahm, with permission.

Figure 191. ***Mesoptychia heterocolpos***, an associate of ***Solenostoma sphaerocarpum*** on stream banks. Photo by Jan-Peter Frahm, with permission.

Figure 192. ***Lophoziopsis excisa***, an associate of ***Solenostoma sphaerocarpum*** on stream banks. Photo by Štěpán Koval, with permission.

Adaptations

Solenostoma sphaerocarpum (Figure 188-Figure 189, Figure 193) is very **polymorphous** (expressing multiple forms). It becomes red-colored in exposed situations (Váňa *et al*. 2013).

Reproduction

Solenostoma sphaerocarpum (Figure 188-Figure 189, Figure 193) is **heteroicous** (male & female organs on same plant; Figure 193), leading to its classification among several species, including ***S. rossicum*** in Russia and ***S. pyriflorum*** subsp. ***purpureum*** in west Greenland. Newton (1983) followed the spore germination and sporeling development. She found up to six gametophytes could be produced by one protonema. It is interesting that in mature leaves the oil bodies were fewer, but larger, when compared with immature leaves and protonemata. It is one of the few liverworts to possess purple rhizoids.

Figure 193. ***Solenostoma sphaerocarpum*** with perigynia visible. Photo by Hugues Tinguy, with permission.

Solenostoma stephanii

(syn. = *Aplozia stephanii*)

Distribution

Solenostoma stephanii occurs in Australia, Oceania, and southern Asia (ITIS 2020).

Aquatic and Wet Habitats

Ruttner (1955) reported ***Solenostoma stephanii*** as submersed in the **littoral** (relating to or situated on shore of sea or lake, usually shallow) zone in the tropics.

Solenostoma tetragonum

(syn. = *Nardia tetragona*)

Distribution

Solenostoma tetragonum is known from Australia, Oceania, and southern Asia (ITIS 2020p). This includes southeast Asia, from Himalayas, India, and Srí Lanka to China, Japan, Micronesia, Samoa, New Guinea, and northern Australia (Li & Váňa 2015).

Aquatic and Wet Habitats

The only wetland study that lists ***Solenostoma tetragonum*** is that of Ruttner (1955) for **tuff** (fine-grained volcanic rock) walls in the tropics. Gupta and Asthana (2016) list this species for soil and dry or wet racks at mid and upper altitudes.

Some people have found this liverwort to be desirable for aquaria (Elo500 2014), indicating its ability to be aquatic.

Solenostoma truncatum (Figure 194)

(syn. = *Nardia truncata*)

Distribution

Solenostoma truncatum (Figure 194) is widespread mostly in southeastern Asia and northern Australia (Li & Váňa 2015). It is very variable in leaf shape, cell texture, and perianth characters (Li & Váňa 2015), resulting in many synonyms (*e.g.* Váňa & Long 2009; Li *et al*. 2017).

Figure 194. ***Solenostoma truncatum***, a species mostly from southeastern Asia and northern Australia, occurring on wet rocks, moist soil, and sulfur springs, as well as some drier habitats. Photo from Hong Kong Flora, with permission.

Aquatic and Wet Habitats

Ruttner (1955) reported ***Solenostoma truncatum*** (Figure 194) as a species of sulfur springs in the tropics. Li and Váňa (2015) considered it to be the commonest species of ***Solenostoma*** in southeast Asia. In the Ghats of India it grows on moist soil in shady habitats, either in pure patches or with other bryophytes, expressing the variety ***kodaikanalensis*** (Alam *et al*. 2012).

The species occurs on soil, wet rocks, and soil-covered rocks at middle and upper altitudes in the Pachmarhi Biosphere Reserve, India (Gupta & Asthana 2016).

Solenostoma vulcanicola (Figure 195-Figure 196)

(syn. = *Jungermannia vulcanicola*, *Nardia vulcanica*)

Distribution

Solenostoma vulcanicola (Figure 195-Figure 196) has a relatively small distribution in Indonesia, Japan, and India (Singh & Singh 2015).

Figure 195. ***Solenostoma vulcanicola*** removed from clump to show individual plants. This species has a limited distribution in Asia and is restricted to sulfur springs. Photo courtesy of Angela Ares.

Figure 196. ***Solenostoma vulcanicola*** showing dense clumps from an acid spring in Japan. Photo by Juuyoh Tanaka, through Creative Commons.

Aquatic and Wet Habitats

In 1955, Ruttner listed ***Solenostoma vulcanicola*** (Figure 195-Figure 196) as one from sulfur springs in the tropics. Satake and coworkers have published multiple papers on its tolerance of the chemistry of Japanese springs and spring-fed streams (Satake 1983). It is able live and thrive in a *p*H range of 3.6 to 4.6, disappearing at 5.5 (Satake *et al*. 1989). In fact, it has not been recorded at a *p*H above 4.6, but it is known from Kusatsu hot spring (Japan) at *p*H 1.9! At such low *p*H levels, iron oxide accumulates on the shoots and is difficult to remove. Potassium in the shoots reached as much as 5%.

Bacteria can occur in the cell wall of ***Solenostoma vulcanicola*** (Figure 195) in acid (*p*H 4.2-4.6) stream water (Satake & Miyasaka 1984b), suggesting a possible role in decomposition.

Satake (1983) explored the accumulation of various elements in stream waters and in their bryophytes. Satake *et al*. (1989) demonstrated that few species were able to tolerate a variety of heavy metals in their water environment. ***Solenostoma vulcanicola*** (Figure 195-Figure 196), growing in a *p*H range of 4.0-4.6, were covered with a precipitate of $Fe(OH)_2$ that accounted for 5-13% of its dry weight. Its K accumulation was up to 5%.

Shiikawa (1956, 1959, 1960, 1962) found that the liverwort ***Solenostoma vulcanicola*** (Figure 195-Figure 196) plays an active role in deposition of iron ore. Since Japan has few native sources of usable iron, Ijiri and Minato (1965; Wickens 2001) suggested producing limonite ore artificially by cultivating this liverwort and other bryophytes in fields near iron-rich springs.

Satake and Miyasaka (Satake & Miyasaka 1984a; Satake *et al*. 1990) reported the accumulation of mercury in ***Solenostoma vulcanicola*** (Figure 195-Figure 196) from a stream (Figure 1) at *p*H 4.2-4.6. Satake *et al*. (1983; 1984) found the highest mercury content (12,100 Hg g^{-1}) in basal segments (1.3%, Satake 1985) of ***Solenostoma vulcanicola*** from an acidic stream in Japan (Figure 1). Satake and coworkers demonstrated that mercury is accumulated from stream water primarily in the cell walls of this species (Satake *et al*. 1983, 1988, 1990; Satake & Miyasaka 1984a; Satake 1985), and not in the **plasmalemma** (cell membrane) or chloroplasts (Satake & Miyasaka 1984a).

The mercury forms electron-dense particles as a mercury-sulfur compound, probably mercuric sulfide, which is not toxic to living organisms.

In addition to mercury, ***Solenostoma vulcanicola*** (Figure 195) from rivers, streams, lakes, and springs accumulates scandium (Satake & Nishikawa 1990). Among the 18 bryophytes analyzed, only this species and ***Scapania undulata*** showed a substantial accumulation.

Adaptations

Solenostoma vulcanicola (Figure 195) can become brownish black to black (Figure 197), but not red or purple (Bakalin 2014). Their stems are mostly erect, permitting them to form tight cushions (Figure 196-Figure 197). The rhizoids are sparse.

Reproduction

Solenostoma vulcanicola (Figure 195) is **dioicous** (Bakalin 2014). Despite the difficulty of its sexual reproduction, it can form huge cushiony mats in the right conditions (Figure 1, Figure 197).

Figure 197. ***Solenostoma vulcanicola*** habitat showing extensive cushions. Photo courtesy of Angela Ares.

Summary

The **Jungermanniineae** are represented by 11 families in wet and aquatic environments. Some of these, such as ***Jungermannia exsertifolia***, ***Marsupella aquatica***, ***M. sphacelata***, ***Nardia compressa***, and ***Solenostoma vulcanicola*** can be classified as truly aquatic, only occasionally being out of water, although they may occur on emergent rocks where they are constantly saturated. The others in this subchapter occur in wet habitats, but are not restricted to aquatic habitats.

The **Jungermanniineae** typically grow in mats, but several grow among or on ***Sphagnum***. Some are known to host fungi. They often have terpenoids that may serve as antibacterial and antiherbivore agents. Their protective coloration seems to go more to brown than red, but some species do form red pigments.

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